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# FIFTEEN- AND SIXTEEN-CHROMOSOME OENOTHERA MUTANTS[1]

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## *A*. INTRODUCTION

The present communication is the second of a series of three, the first having been published in a preceding issue of this JOURNAL[2] under the head of "Mutants of Oenothera with diminutive chromosomes." The three papers embody a portion of the results derived from a prolonged study of the Lamarckiana group of Oenothera conducted at the Station for Experimental Evolution[3] (1907–1911), at the University of Louvain in Professor V. Grégoire's laboratory (1911–1912), and later in consultation with Professor Grégoire by letter (1912–1914).

As stated in the first report of the series, the primary object of these communications is to discuss, in the light of the Cold Spring Harbor and Louvain studies, certain theories and conclusions which Gates has given out from time to time and which Gates and Miss Thomas ('14) have based upon the results of their investigations.

The first paper described an interesting condition found in two mutant types produced by 15-chromosome *O. lata* × 14-chromosome *O. Lamarckiana;* one, a new form, *O. aberrans*, grown at Cold Spring Harbor in 1908 and 1909, and the other, *O. rubrinervis*, grown at Amsterdam in 1912. The somatic cells of these three plants were shown

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[1] Briefly reported in a paper read before the Botanical Society of America, December 29, 1915, and in a preliminary note published in Science (Lutz, '16*a*) entitled "The production of 14+-chromosome mutants by 14-chromosome *Oenothera Lamarckiana*."

[2] Amer. Journ. Bot. 3: 502–526. 1916.

[3] Maintained by the Carnegie Institution of Washington until March, 1911.

[The Journal for January (4: 1–52) was issued Feb. 3, 1917.]

to have fourteen chromosomes of the usual size and one small one. The germ-cells were not examined. The significance of this $14^{+1}$-chromosome condition in offspring of 15-chromosome mothers was discussed in relation to the discoveries of Geerts, who showed in 1911 that seven of the twenty-one chromosomes of certain hybrids may fragment and degenerate during reduction, and of Gates and Miss Thomas ('14) who demonstrated that one of the fifteen chromosomes of *O. lata* and certain *lata*-like forms may sometimes behave in a similar namner.

In the paper just referred to, Gates and Miss Thomas announced the precise somatic chromosome number of 21 plants falling under the heads of *O. lata, O. semilata* and various *lata*-like forms. The authors found that "all without exception contained 15 chromosomes" and have discussed many new and interesting features "in connection with the behaviour of the extra chromosome and the phenomena of degeneration." Their researches appear to have led them to conclude that the presence of the extra chromosome in 15-chromosome offspring of 14-chromosome forms is invariably associated with *lata* or *lata*-like characters in the soma of the mutant. Later Gates ('15*a*, pp. 147–148) described a 15-chromosome mutant which he showed had a few characters in common with *O. lata* and many others which were quite unlike those of the latter form. It appears, however, that he regarded this mutant as a *lata*-like form, since nowhere in this work has he intimated that the discovery of 15 chromosomes in *O. incurvata* has modified his previously expressed views concerning the relation of *lata* characters to the extra chromosome. In March of the same year de Vries ('15*a*, p. 187) described two types of offspring, besides a mutant which Stomps had obtained from *O. biennis semigigas* pollinated without castration by pure *biennis*. One of the two types, represented by 8 individuals, had 15 chromosomes and he calls attention to the fact that while these plants had the same number of chromosomes as *O. lata, they had none of the characters of the latter form.* In December following Gates ('15*b*) recognized the fact that his mutant *O. incurvata* is quite different from *O. lata*, as is also the 15-chromosome form which de Vries reported. He adds: "Hence we may say that whenever a germ cell having 8 chromosomes fertilizes a normal germ cell a new form is produced, though what its characters will be depends upon various circumstances which need not be considered here. One of the most important of these factors is probably the peculiar combination of chromosomes received." He does not state, however, that these discoveries render untenable certain earlier conclusions of Gates and of Gates and Miss Thomas concerning the relation of the extra chromosome to *lata* and *lata*-like characters, but takes what appears to be a last brave stand to save the day in the statement which follows the words quoted above: "It is perhaps not inappropriate to speak of all these mutants as belonging to the *lata* series, or the series with an extra chromosome." It must be conceded, however, that a plant which de Vries clearly states has none of the characters of *O. lata*, can not logically be held to belong to the *lata* series of mutants. Furthermore, it has been shown in the note which preceded this publication (Lutz, '16*a*) that a number of distinct mutant forms, quite unlike *O. lata*, have been found by the writer to have 15 chromosomes. The chromosome number of each of the 9 un*lata*-like types reported was ascertained, and their dissimilarity to *O. lata* fully recognized, previous to the year 1913.

The primary object of this paper, therefore, is to discuss Gates's and Gates and Miss Thomas's theories and conclusions regarding the extra chromosome at length in the light of the fact that many un*lata*-like 15-chromosome mutants are now known and that many more doubtless exist, in order that it may be shown that many of their conclusions are untenable.

## *B.* 15-CHROMOSOME MUTANTS

### 1. *Has* O. lata *14 or 15 Chromosomes? Is the Number of Somatic Chromosomes Inconstant in this Form?*

For a period of four or five years following the announcement of the somatic chromosome number of *O. Lamarckiana* by Geerts in 1907, all mutant offspring of *O. Lamarckiana*, with the exception of *O. gigas*, were supposed to have the same number of chromosomes as the parental form; namely, fourteen. Fifteen chromosomes had been reported for *O. albida*[4] in one of the earlier notes published by the writer (Lutz, '08), but the discovery was not emphasized and doubtless was overlooked, with the result that *O. gigas* continued to be regarded as the sole mutant derivative of *O. Lamarckiana* with a chromosome number differing from that of the parental form.

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[4] Two plants. Notwithstanding the fact that they were offspring of *O. lata* × *O. Lamarckiana*, they were mutants, since *O. albida* was not employed as either parent.

In the year following that in which the note was published concerning *O. albida*, it was announced that 15 chromosomes had been counted in two *lata* offspring of *O. lata* × *O. gigas* (Lutz, '09). These plants, of course, were not mutants, but it did not seem unreasonable to suppose that mutant *lata* would be found to have the same number of chromosomes as the hybrids. Gates, however, had repeatedly announced 14 as the sporophyte number for *O. lata* and the evidence produced seemed quite sufficient to support his claims. In a preliminary note published in 1907[5] he said (p. 260): "The sporophyte number of chromosomes in *O. lata* . . . is 14." Speaking of *O. lata* in the detailed report which followed,[6] he said (p. 92): "It has been determined *from a number of counts* in the prophase that the sporophyte number of chromosomes . . ., is 14." (Italics not employed in the original.) Again, later in 1907[7] (p. 9), "In *O. lata* the count of chromosomes was made in the pollen mother cells and found to be fourteen. It has since been made in various somatic tissues of the flower, and is found to be constantly fourteen so far as observed. *There has been no indication whatever that the number is ever higher.*" (Italics not employed in the original.) Again, on page 11, "Several plants of *O. lata* and the pure *O. Lamarckiana* have been examined, all having fourteen chromosomes."

As earlier stated, the primary object of the Cold Spring Harbor studies of Oenothera, begun in 1907, was to ascertain whether or not each particular combination of somatic characters, such as that represented by the type we know as *O. lata*, for example, is associated with a definite, fixed number of somatic chromosomes; in other words, whether or not somatic chromosome number in Oenothera is constant. Years of careful study, by the writer, of the vegetative characters of plants from seedling to fruiting stage (never overlooking the importance of taking note of the slightest deviation from the combination represented by the type) together with the precise determination of somatic chromosome number in over 200 individuals, established the fact that each combination of somatic characters is constantly associated with a certain number of chromosomes; in other words, that each type of plant has a definite, fixed number of chromosomes. It was therefore announced in "Triploid mutants" (Lutz, '12), and many times emphasized throughout the report (pp. 390, 416, 418, 420) that *all individuals having identical somatic characters from seedling to fruiting stage invariably have identical somatic chromosome numbers, regardless of the parentage or the origin of the plants in question.* Owing to the contradictory nature of the evidence produced by Gates and Lutz relating to somatic chromosome number in *O. lata*, it was feared that this type might be regarded as an exception to the rule.[8] It was therefore stated (p. 416) that the Cold Spring Harbor studies had established the precise somatic chromosome number of 28 latas; that each had been found to have 15 chromosomes, "whether mutant, hybrid, offspring of mutant *lata* self-pollinated, or offspring of hybrid *lata* self-pollinated; whether grown at Amsterdam, Cold Spring Harbor, or the New York Botanical Garden; and whether derived from de Vries's cultures, from plants descended from plants or seeds from de Vries, or from plants of English ancestry, in no wise related to de Vries's cultures."

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[5] Gates, '07*a*.

[6] Gates, '07*b*.

[7] Gates, '07*c*.

Later in the same year in which the above announcement was made, Gates ('12) stated that he had counted the chromosomes in one *lata* plant and had found the number in this individual to be 15, and added (p. 995): "From all the counts thus far made of the chromosomes in *O. lata* it appears that the number 15 occurs at least in most individuals, though the counts are perhaps not yet numerous enough to show that 15 is the number for all individuals, . . ." From a note added at the conclusion of this report, it seems that the statement concerning *O. lata* in "Triploid mutants" had not appeared in print or had not attracted his notice at the time this communication was sent to press. In the note he says that the preparations of *O. lata* described in his first paper on the subject were re-examined, but that they had deteriorated somewhat and he was "unable to determine with certainty whether this *lata* plant contained 14 or 15 chromosomes."

Since Gates's early statements were clearly based upon a number of counts, it seems improbable that the extra chromosome, if present, would have repeatedly escaped his notice. Owing to an unfortunate error in identification during the first year of the work, Lutz ('08) had announced 14 chromosomes for a plant supposed to be *O. lata*, but later shown to be a distinct type.[9] It is possible, therefore, that Gates mistook some *lata*-like form having 14 chromosomes, for *O. lata*. The number of individuals in which he counted 14 chromosomes is not known; it is clear from the note referred to at the end of the preceding paragraph, that only one plant was mentioned in the first two 1907 papers, but his statements in the third that "Several plants of *O. lata* and the pure *O. Lamarckiana* have been examined, all having fourteen chromosomes," certainly indicates that 14 had been counted in more than one individual identified as *O. lata*. At any rate, Gates appears to be convinced of error in count or identification in his early studies of *O. lata*, since he states ('13, pp. 301–302) that Gates and Miss Thomas's studies of *O. lata*, etc. "corroborated the independent results of Miss Lutz and Gates regarding the constancy of the fifteen chromosomes in *O.* mut. *lata*, . . ." Furthermore, Gates and Miss Thomas ('14) not only emphasize the constancy of the 15-chromosome condition in *O. lata* without reference to the earlier count of 14, but appear to be convinced that plants having 15 chromosomes invariably have *lata*, *semilata*, or *lata*-like characters. In fact, in Gates's recent work ('15*a*, pp. 167 and 296) he says, in referring to the *lata* plant discussed in his first two 1907 reports, that his discoveries indicated

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[8] One may be led to inquire also whether $14^{+1}$-chromosome forms may not be regarded as exceptions to the rule. In considering this question it should be borne in mind that we do not yet know whether the small member of the chromosome group is constant or variable. Should future studies show the latter to be true, we should then be called upon to decide whether these $14^{+1}$-chromosome forms should be regarded as actual exceptions to the rule, since the small body is, in all probability, not a chromosome, but merely a detached fragment of a whole chromosome, or a remnant of a degenerating chromosome.

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[9] Certain forms which were studied during the first years of the writer's work are now known to have been erroneously classified (see '12, p. 390, note 11, and 16 *b*, p. 514, note 7). The reappearance of the 14-chromosome form supposed to be *O. lata* has shown that this mutant was not *O. lata*, though resembling it strongly in early rosette characters (to be demonstrated in a later publication). The 16th chromosome of one figure of a second *lata* has since been demonstrated to me by Professor Grégoire to be merely a deceptive anastomosis between two parallel chromosomes although Gates ('12) has since reported two 16-chromosome cells in a 15-chromosome *lata* and one 16-chromosome cell has also been found in a C. S. H. *lata*. The 15-chromosome form called *O. nanella* was a dwarf, not *O. nanella*. Likewise, it has since been demonstrated that the 14- and 15-chromosome forms designated as *oblonga* did not duplicate each other and that the first type is certainly not *oblonga*, though *oblonga*-like, and the second (type 5509) may be *oblonga* but is believed to be a modified form of de Vries's mutant. The latter type has continued to appear in *Lamarckiana* and other cultures since 1908. These errors of identification were the result of premature publication of inexperienced work and are most regretable, as they serve only to mislead others. By withholding later publications until identifications and results of investigations could be verified, it is hoped that similar errors have been avoided.

"about" 14 chromosomes, but that the number for *O. lata* has since been shown by Lutz, Gates, and Gates and Miss Thomas, to be 15.

These facts are outlined at length in order that the reader may understand that mistaken identification of one plant by Lutz and possible mistaken identification or error in count by Gates are responsible for the early statement that *O. lata* had 14 chromosomes. It may be assumed with safety now that the number of somatic chromosomes present in the type of *O. lata* produced by *O. Lamarckiana* is invariably 15.

### 2. O. lata *and the "Extra" Chromosome*

In "Recent papers on Oenothera mutations" Gates ('13, pp. 301–302), as stated above, mentions the then unpublished results of investigations conducted by Gates and Miss Thomas ('14) which had disclosed 15 chromosomes in 21 plants classified by them as *O.* mut. *lata*, *O.* mut. *semilata*, *O. lata* to *semilata*, *O.* mut. *lata rubricalyx*, *O. biennis* mut. *lata* and as *lata*-like forms. Referring to *O. lata rubricalyx* which appeared among the $F_2$ offspring of two 14-chromosome forms crossed (*O. rubricalyx* × *O. grandiflora*), he says: "The possession of fifteen chromosomes by this plant also shows that whenever a meiotic irregularity leads to the formation of an individual having an extra chromosome, such a plant will have the leaves and habit of *lata* or *semilata*." Although he adds in a footnote that "It is possible that one or two other mutants also have an extra chromosome," he does not state or intimate that such forms are not *lata*-like; furthermore, Gates and Miss Thomas say in the later report (pp. 551–552), "Certain other mutants indicate by their hereditary behaviour that they may also have aberrant chromosome numbers, but this has not yet been proved, except in *gigas*."

Gates was the first to show that one of the heterotypic chromosomes of a form may pass "into the same daughter-nucleus as its mate, instead of into the opposite nucleus." He first demonstrated this significant irregularity in 14-chromosome *Lamarckiana* in 1907, but has since observed the same peculiarity in many other forms. With reference to this occasional 6–8 distribution of heterotypic chromosomes in 14-chromosome forms, Gates and Miss Thomas say (p. 550): "Whenever this irregular meoitic division occurs in a pollen mother-cell, such a cell will, at least in many cases, give rise to two *lata*-producing pollen grains in addition to two having only 6 chromosomes. The latter apparently always degenerate. Similarly, when such an irregularity occurs in the megaspore meiosis, if the 8-chromosome megaspore functions it will, after fertilisation by a 7-chromosome pollen grain, give rise to a *lata*-like mutant. . . . Moreover, in *lata* or *semilata* when crossed with their 14-chromosome parents or when self-pollinated, the percentage in which the mutant reappears will depend upon the relative number of their 8-chromosome and 7-chromosome germ-cells which function."

The authors then state that the frequency of this unequal division appears, from the observations of Gates to be "of the order of 1 per cent." This, they say, would give about two 8-chromosome pollen grains in 400, or 0.5 percent, and that "If the frequency of this irregularity in the megaspore mother-cells is the same, about 1 per cent. of *lata* mutations should be anticipated."

Gates's claim that "whenever a meiotic irregularity leads to the formation of an individual having an extra chromosome, such a plant will have the leaves and habit of *O. lata* or *O. semilata*" leaves no loophole for escape from the conclusion that all 15-chromosome offspring of 14-chromosome forms—or at least all which are derived from the fertilization of an 8-chromosome egg by a 7-chromosome sperm —"have the leaves and habit of *O. lata* or *O. semilata*," while Gates and Miss Thomas's estimates of the percentages of offspring of *O. lata*, selfed, and of *O. lata* × *O. Lamarckiana* which may be expected to reproduce the characters of *O. lata*, lead the reader to conclude that progeny resulting from 8 + 7 unions invariably have the characters of *O. lata*, *O. semilata*, or some *lata*-like form.

All of the 15-chromosome mutants which Gates and Miss Thomas mentioned in this report and which Gates has discussed in earlier publications, were classified as *O. lata*,[10] *O. semilata*, *lata* to *semilata* or *lata*-like forms, and it appears that these were the only 15-chromosome mutants whose somatic chromosome numbers had been ascertained by them at that time;[11] if such be the case, this chance occurrence is probably responsible for their conclusions. That many of the 15-chromosome mutant offspring produced by 14-chromosome forms have *lata* or *lata*-like characters cannot be questioned, but it is equally certain that a far greater number do not. It seems to the writer that the authors' announcements were a bit premature in view of the fact that the somatic chromosome numbers of so many mutant offspring of 14-chromosome *O. Lamarckiana* had not been reported. For example, the somatic chromosome numbers of *O. scintillans*, *O. spathulata*, *O. elliptica*, *O. sublinearis*, *O. leptocarpa*, *O. subovata*, etc., all *Lamarckiana* mutants, had not been announced at that time. The same is true of *O. nanella lata*,[12] *O. nanella oblonga* and *O. nanella elliptica*—compound types appearing in 14-chromosome *O. nanella* cultures and elsewhere. Furthermore, as previously stated, it has been shown (1908) that *O. albida*, one of the very common *Lamarckiana* mutants, is a 15-chromosome form, yet this plant cannot be listed either as *O. lata* or as a *lata*-like form.

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[10] Including *O. lata rubricalyx* and *O. biennis lata*.

[11] As we have seen, Gates ('15*a*) has since reported a 15-chromosome mutant, *O. incurvata*, which still later ('15*b*) he says is quite different from *O. lata*.

I have studied the somatic chromosomes of 305 plants of the *Lamarckiana* group and have determined the precise number of 234 individuals. Exclusive of the two $14^{+1}$-chromosome mutant types mentioned in the preceding report, of the offspring of *O. lata* × *O. gigas*, *O. Lamarckiana* × *O. gigas*, *O. nanella* × *O. gigas* and of *O. gigas*, selfed, *16 distinct mutant types were found among these 234 individuals (17 among the 305) having more than 14 chromosomes; 11 of the 16 were 15-chromosome forms, 3 were 16- and 2 were triploid. The 17th type having 14+ chromosomes was also a triploid form.* In addition to the above, one type having a number of characters in common with one of the eleven 15-chromosome types mentioned, was also found to have 15 chromosomes. Also, 15 chromosomes were repeatedly counted in root-tips from a mutant grown at Amsterdam in 1912 and identified by Professor de Vries as *O. oblonga*, but a certain irregularity found in several tips of the plant (to be described later) indicated a possible abnormal condition and made it seem inadvisable to accept the count in this individual as typical of the species until verified by counts in other oblongas.[14] Besides the 11 or 12 types which were ascertained, beyond doubt, to have 15 chromosomes, 2 quite distinct types had 15(?) chromosomes (number not determined precisely).

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[12] Hunger ('13) found plants which he identified as *O. lata nanella* and *O. oblonga nanella* in cultures of *O. Lamarckiana*.

[13] I have since verified this count in 13 additional *albida* mutants.

[14] Professor de Vries has kindly aided me in every way to determine the precise number of chromosomes in the Amsterdam type. In the early summer of 1915 he sent me a number of young *oblonga* rosettes from his gardens, but, unfortunately, all perished before reaching their destination. He also sent me a generous supply of seeds from one of his best plants, but very few of these germinated and only one seedling survived. Root-tip fixations were prepared from this plant, but no satisfactory counts have been obtained from them thus far.

We may now consider, briefly, the evidence furnished by these 15- and 15(?)-chromosome forms.

(*a*) *Distinct Types Having 15 Chromosomes.*—Four of the 11 distinct types are very common *Lamarckiana* mutants, though found in other cultures, as well: (1) *O. lata*, (2) *O. albida*, (3) *O. bipartita* (C.S.H.) and (4) type 5509 (C.S.H.), supposed to be a modified form of de Vries's *oblonga*. Among the less common forms are (5) *O. nanella lata*,[15] obtained from de Vries's culture of *O. lata* × *O. Lamarckiana* (1912), but found also in cultures of *O. Lamarckiana*, *O. nanella*, etc. (6) *O. subovata*, obtained from *O. lata* × *O. Lamarckiana*, but also produced by *O. Lamarckiana*. (7) A dwarf mutant, type 2256, found in a culture of *O. nanella*, (8) type 4499, produced by *O. lata*, selfed, and *O. lata* × *O. Lamarckiana;* and three mutants which have been observed in *lata* cultures only, thus far: (9) *O. exilis*, (10) *O. exundans* and (11) type 5365.

*O. bipartita* is a remarkably beautiful and interesting form. The peculiarities of the young plant not yet come to flower are shown in Figure 1. The leaves, particularly those of the young plants, are thin and papery feeling; those of the adult form being more crinkled and more finely crinkled, being somewhat broader in proportion to their length, than *Lamarckiana* leaves. Although *bipartita* attains the height of the tallest *Lamarckiana*, it is more dainty in appearance than the parental form (Fig. 2). Like the latter, it produces a circlet of basal branches which are somewhat shorter and less decumbent than the rosette branches of *Lamarckiana* (Fig. 3). Not only are the branches more slender, but the buds, which are regular and tapering, are shorter and the flowers smaller than in the case of *Lamarckiana*.

*O. bipartita* is distinguished by the large number of flowers produced having more than 4 regular, tapering, stigmatic rays. Flowers with 4+-rayed stigmas are common to most forms, yet the number of flowers produced daily by *bipartita* having 4+-rayed stigmas forms a higher percentage of the total than has been found to be true of any other one of the freely blooming plants. The percentage of flowers having 4+-rayed stigmas varies greatly among the individuals of a given type. Daily records were made during the greater part of a

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[15] Professor de Vries states that he uses the term "*O. lata nanella*" and "*O. nanella lata*" interchangeably.

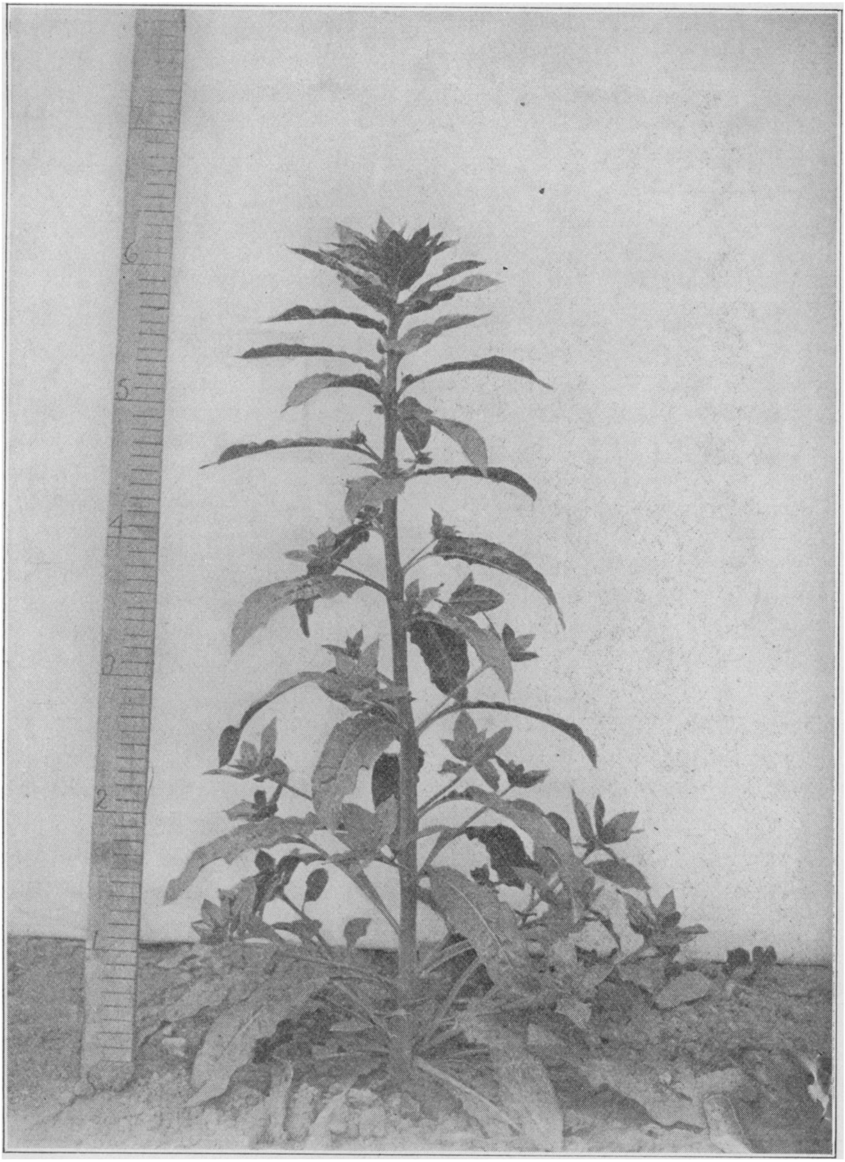

FIG. 1. *O. bipartita*, plant No. 5561. C.S.H., 1910. Mutant offspring of *O. Lamarckiana* × *O. Lamarckiana*. Not yet come to flower.

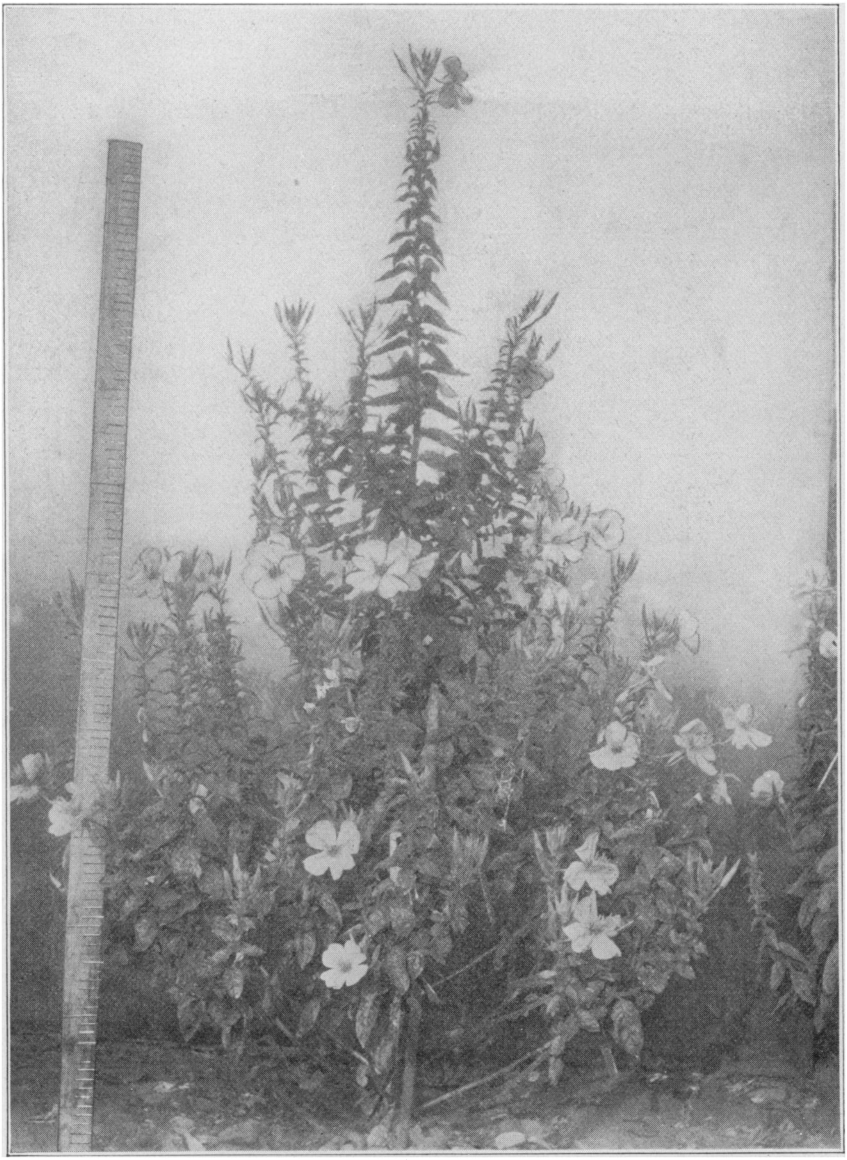

FIG. 2. *O. bipartita,* plant No. 5561, at height of flowering period. One of the two uppermost flowers shows cleft petal.

flowering season of the flowers produced by two biennial Lamarckianas, and it was found that a larger percentage of the early, than of the late, flowers had 4+-rayed stigmas.

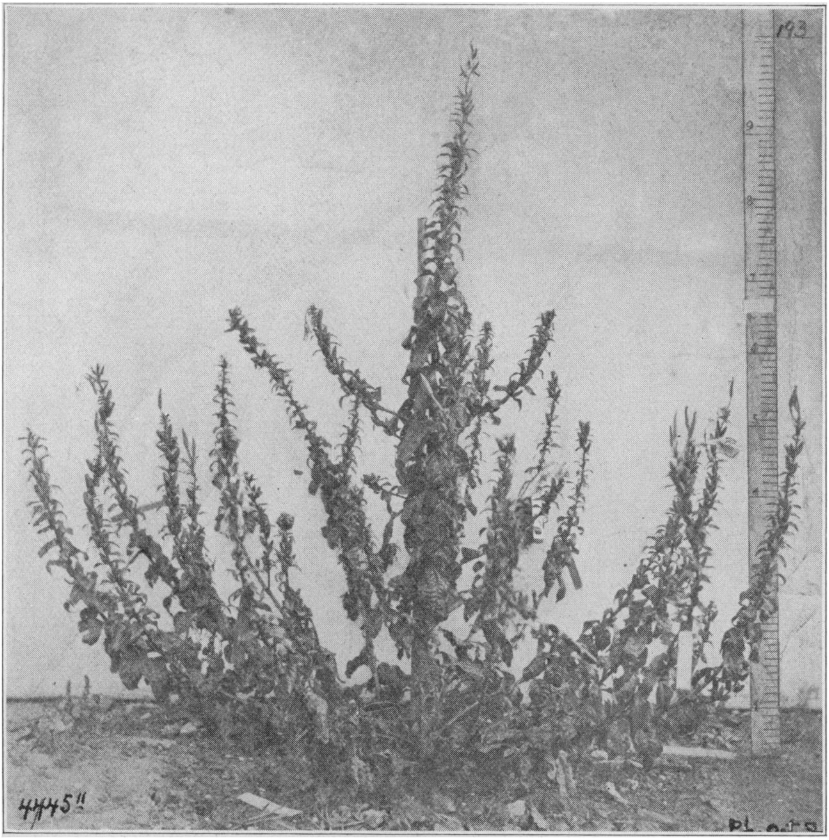

FIG. 3. *O. Lamarckiana*, plant No. 5958, C.S.H., 1909. Offspring of *O. Lamarckiana*, selfed. Photographed late in the season to show manner of branching.

This seemed to be due to a tendency on the part of the first flowers of the stem and vigorous rosette and stem branches to have 4+-, rather than 4-rayed stigmas, though flowers with 4-rayed stigmas were common among the first, and flowers with 4+- were frequently found near the terminal portions of these parts. After the plants had bloomed a short time, it was found that the number of flowers having 4-rayed stigmas exceeded the number of those having 4+-, and towards the close of the flowering season it was seen that the number of the former greatly exceeded that of the latter.

On a certain day, at the height of the flowering season of 1910, 62 flowers unfolded on one *bipartita* mutant, and 52 of these had 4+-rayed stigmas. On August 31 of the same year, 80 percent of the 214 flowers produced by 9 *bipartita* mutants had 4+-rayed stigmas, while less than 1 percent of the 312 produced by 9 Lamarckianas selected at random on the same day, were distinguished in this manner. All had been in flower about the same length of time.

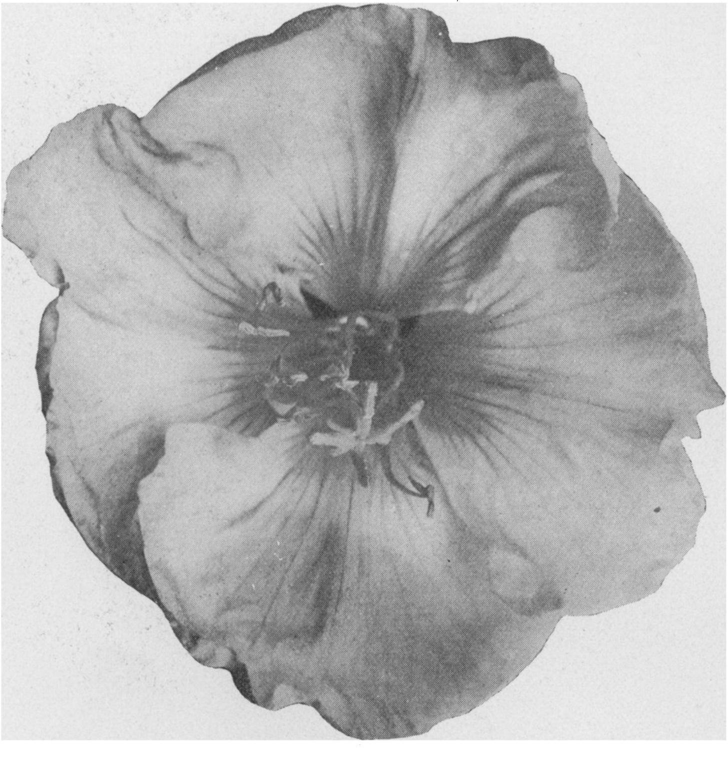

FIG. 4. $F_2$ *O. lata* × *O. gigas*, plant No. 4930, C.S.H., 1909. Flower showing normal arrangement of petals.

When a bud is held with the apex of the cone upward and the sepals are then stripped backward, it will be found that the petals are rolled, in the majority of cases, from left to right (viewed from the sepal side) with the right lateral margin free and the left overlapped by the right lateral of the preceding petal (Fig. 4). Occasionally, when a bud opens, it is found that the relative positions of the right and left margins of two neighboring petals are reversed, the left of one overlapping the right of the other. A few buds have been found in which a complete reversal of relative positions had occurred at all four points; commonly this takes place at but one. Complete reversal produces no disturbance, but partial reversal frequently, though by no means invariably, causes interference in the growing bud. For example, when the left lateral margin of a petal, which we may designate as 2, becomes dis-

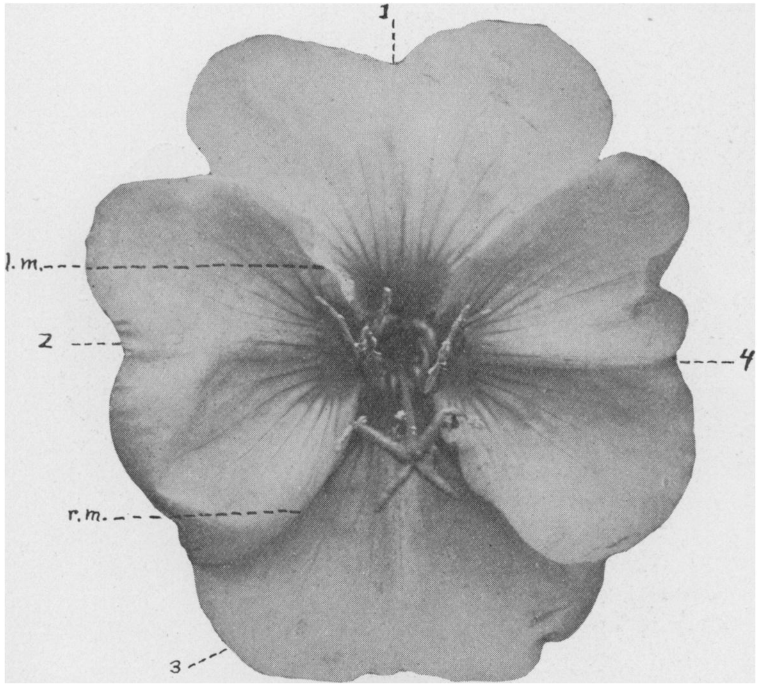

FIG. 5. $F_1$ *O. Lamarckiana* × *O. gigas*, plant No. 3750, C.S.H., 1908. Flower showing reversed petal arrangement at two points, the left lateral margin of petal 1 (*l. m.*) overlapping the right lateral of 4 (*r. m.*) and the left of 3 overlapping the right of 2, leaving petals 2 and 4 in, and 1 and 3, out.

placed and overlaps the right lateral margin of petal 1, both lateral margins of petal 1 are left in (Fig. 6), and both of petal 2, out. Therefore the left of 2 and right of 4 are both out, and in the growing bud sometimes forms a sort of an X contact along the left distal margin of 2 and right distal of 4.[16] The right distal of 4 may grow on

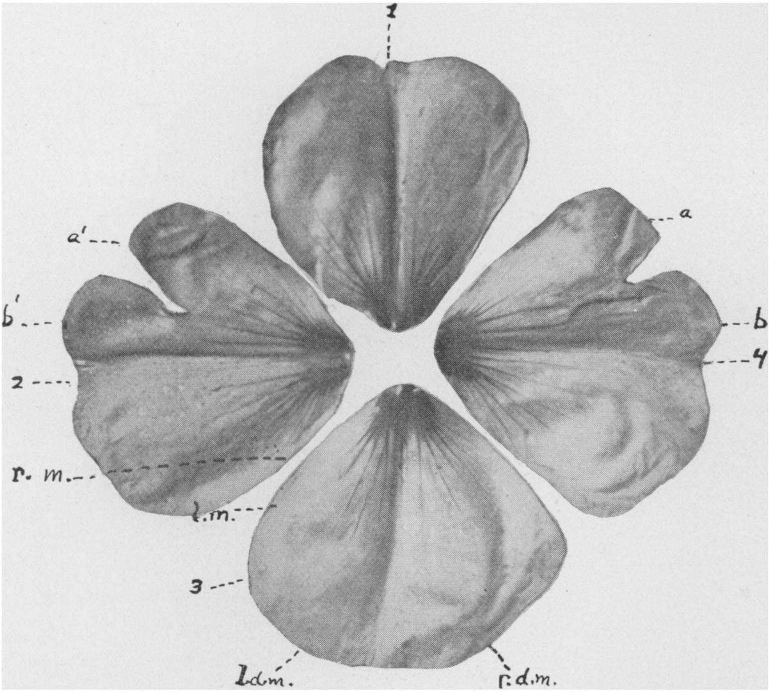

FIG. 6. $F_2$ *O. gigas* × *O. Lamarckiana* (de Vries), plant No. 133(1), Lafayette, Indiana, 1913. Detached petals of flowers showing petal cleavage resulting from reversed petal arrangement at one point, the left lateral margin of petal 2 overlapping the right lateral of 1, leaving both margins of 1 in, and both of 2, out, in open flower. Most common form of irregular arrangement and petal cleavage. *a*, *b* = right distal lobes; *a′*, *b′* = left distal lobes; *r.m.* = right lateral margin; *l.m.* = left lateral margin; *l.d.m.* and *r.d.m.* = left and right distal margins.

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[16] Since Figs. 4, 5 and 6 show flowers photographed from the stigma, instead of from the sepal, surface, the margins which are referred to as right and left in the descriptions of the bud appear in reversed positions when viewed from the inside of the open flowers. The margins are labeled, however, as seen from the sepal surface of the bud.

both sides of the left distal of 2, the latter, as it grows, being crumpled into the slit thus produced by 4. Stripping back the sepals of a bud about to flower, one will find the two petals locked in this manner, the *a* lobe of 4 overlapping the *a′* of 2, and the *b′* lobe of 2 overlapping the *b* of 4.[17] When the flower unfolds, petal 4 may be found with a diagonal slit extending from about the middle of the right half of the distal margin towards the median line of the petal. Petal 2 may or may not have a slit extending from about the middle of the left distal margin towards the median line. It is usually present, and shorter than the slit in petal 4. In the case of the flower shown in Fig. 6, petal 2 has the longer incision, indicating that lobe *a′* of petal 2 overlapped lobe *a* of petal 4, and that lobe *b* of 4 overlapped *b′* of 2. Flowers are found with one, two, three, or all four, of the petals cleft. Sometimes a petal has two slits, one on each side of the median line. In an irregularity such as that first described above, the right margin of 1, as well as the left of 3, is in, consequently these two sometimes interfere, causing an incision either in the left distal margin of 3, or the right distal of 1, or both. Sometimes petal 1, both margins of which are in, wraps around the filaments and anthers. The right and left distal margins may then come in contact in such a way as to cause the two incisions sometimes found in a petal. Not infrequently an irregularity in petal arrangement causes no cleavage. Although cleft petals are sometimes produced by overhanging anthers, in the majority of cases they result from interferences caused by a partial reversal of the direction in which the petals are normally rolled within the bud.

*O. bipartita* is distinguished by the large number of flowers produced with cleft petals. Flowers with cleft petals are found occasionally on individuals of almost any type, including *Lamarckiana*, but they are more common to *bipartita* than any other mutant type observed.[18]

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[17] The petal whose base is attached at the point where the filaments separate is designated as petal 1.

[18] The first flowers of vigorous rosette and stem branches (probably also of the stem) appear to be more subject to this irregularity than those produced by the same parts near the extremity. It is possible also that the first flowers of the short, weak secondary branches produced late in the flowering season are less subject to this irregularity than the first flowers of more vigorous parts, but the facts have not been ascertained regarding this point. The buds of two biennial Lamarckianas were examined daily (with occasional exceptions) throughout the greater part of the flowering season. Plant *A* came to flower June 23 and *B* about the same time. The former was examined for cleft-petaled flowers for the first time on June 29, and the latter on June 28. The results for these days and the 11 and 12 following, were recorded as follows:

Scarcely a day but one or two cleft-petaled flowers were found on each plant, and usually many more. On a certain day, 22 of the 45 flowers produced by one of these mutants had cleft petals. The records for the 9 mutants employed for 4+-rayed stigma counts (see page 66) on the day previously mentioned, August 31, will serve as a typical illustration: 74 of the 214 flowers produced, almost 35 percent, had cleft petals.

The pollen of *O. bipartita* consists of 3-lobed grains. In the buds of the mutants observed it was found to be entirely absent, produced in small quantities, or present in moderate amounts; these conditions were found in the various buds of each plant. A large percentage of the grains produced are bad, and it is exceedingly difficult to obtain seeds from these forms, selfed.

Type 5509, presumably a modified form of de Vries's *oblonga*, seems to bear about the same relation to the Amsterdam mutant as type 3514 (see Lutz, '16*b*) bears to de Vries's *rubrinervis;* yet it is possible that the two are identical forms.

(*b*) *A Related Type, Having 15 Chromosomes.*—Type 2806, a form having many points in common with type 5509. Also found in cultures of *O. Lamarckiana.*

(*c*) *Distinct Types Having 15(?) Chromosomes.*—These are (1) a plant from de Vries's 1912 culture of *O. lata* × *O. Lamarckiana*, said

| | *A* | | | *B* | | |
|---|---|---|---|---|---|---|
| | Total Number of Flowers | Number with Irregular Petal Arrangement | Number with Irregular Petal Arrangement and Cleft Petals | Total Number of Flowers | Number with Irregular Petal Arrangement | Number with Irregular Petal Arrangement and Cleft Petals |
| June 28..... | — | — | — | 30 | 13 | 8 |
| " 29..... | 54 | 3 | 3 | 52 | 4 | 2 |
| " 30..... | 67 | 5 | 5 | 70 | 4 | 4 |
| July 1..... | 63 | 0 | 0 | 82 | 3 | 3 |
| " 2..... | — | — | — | 100 | 10 | 0 |
| " 3..... | 120 | 4 | 1 | 74 | 0 | 0 |
| 4..... | 113 | — | — | 90 | — | — |
| " 5..... | 132 | 1 | 1 | 80 | 0 | 0 |
| " 6..... | 99 | 1 | 1 | 59 | 0 | 0 |
| " 7..... | 59 | 0 | 0 | 45 | 0 | 0 |
| " 8..... | — | — | — | | — | — |
| " 9..... | — | — | — | | 0 | 0 |
| " 10..... | 22 | 0 | 0 | | 0 | 0 |

From July 10 until the close of the flowering season cleft-petaled flowers continued to appear occasionally, but much less frequently than during the early flowering period of the plants.

to have combined the characters of *O. lata* with the smooth, shining leaves of *O. Leata.* (2) *O. elliptica*, a *Lamarckiana* mutant.

Of the 11 distinct types known to have 15 chromosomes, (1) *O. lata*, (2) *O. albida*, (5) *O. nanella lata* and (6) *O. subovata* are well-known forms, originally described by de Vries; (4) type 5509 was mentioned in an early note (Lutz, '08); (7) type 2256, as previously pointed out, was erroneously identified in 1908 as *O. nanella.* All of the remaining five forms are new. The somatic chromosome numbers of *O. lata*, *O. albida*, types 5509 and 2256 were reported in early notes by Lutz; those of *O. bipartita*, *O. nanella lata*, *O. exilis*, *O. subovata*, *O. exundans*, types 4499 and 5365 were communicated in the preliminary note to this paper (Lutz, '16*a*).

A mutant of the *Lamarckiana* group is distinguished from the parental form and other mutants, not so much by some particular character—for few characters are peculiar to any one type alone—as by the combination of characters which is peculiar to itself. Thus, *O. lata* has broad, heavily crinkled leaves, irregularly shaped buds (particularly true of the early buds), light yellow flowers with crumpled petals, barren anthers, etc. No one of these characters is peculiar to *O. lata* alone. The cleft petals and large percentage of flowers having 4+-rayed stigmas are striking characters of *O. bipartita*, yet neither is peculiar to this form alone; it is the combination of characters previously enumerated which distinguishes it from all other forms. A very striking illustration of this point may be found in the previously mentioned 15-chromosome mutant reported by Gates ('15*a*, pp. 147–148), namely, *O. incurvata.* His illustrations and descriptions of this form clearly show that it is not entitled to be regarded as a *lata*-like form, for, although he states that it agrees with *O. lata* "in the obtuse tips and deep crinkling of the leaves," he also says that it differs from *O. lata* "(1) in the much narrower leaves with long petioles, (2) in having one edge of the leaf characteristically folded over, (3) in being as tall as *Lamarckiana* with long internodes, (4) in having more squarish buds which produce pollen." If, in connection with these statements, one compares his photographs of *O. incurvata* (Figs. 56 and 57) with that of *O. lata* (Fig. 37), all in the rosette stage, one will see that *O. lata* and *O. incurvata* are about as unlike as any two mutants which may be mentioned. It is quite clear that the "obtuse tips and deep crinkling of the leaves" do not entitle this form to be regarded as *lata*-like, since it is wholly unlike

*O. lata* in the majority of its characters. The tendency of the margin of the leaves of *incurvata* to roll towards the upper surface of the midrib is one of the most striking characteristics of the full-grown rosette leaves of *O. albida* (compare Fig. 7 with Gates's Fig. 56).

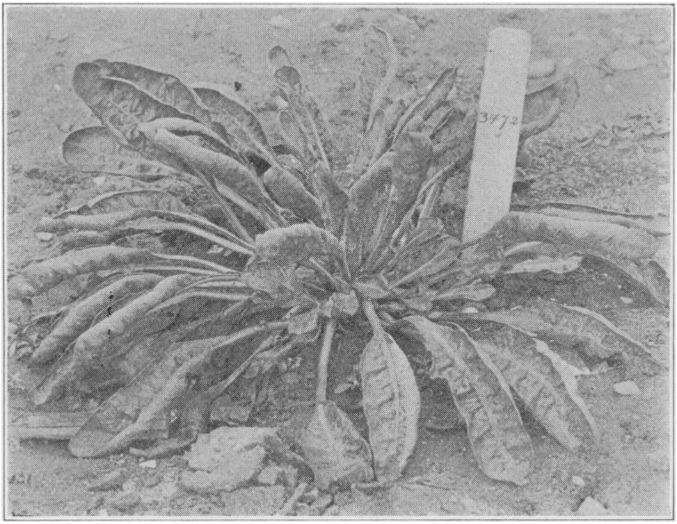

FIG. 7. *O. albida*, plant No. 3472, C.S.H., 1908. Offspring of *O. Lamarckiana* × *O. Lamarckiana*. Mutant in late rosette stage showing margins of leaf blade rolling towards the midrib; a typical *albida* character.

In view of the above facts, it is not surprising to find that a few of the twelve 15-chromosome types had one or two characters suggestive of *O. lata*, just as others had one or two suggestive of *O. Lamarckiana*, of *O. rubrinervis* or some other form; yet, since the majority of the characters were wholly unlike those of *O. lata* in the first case and wholly unlike those of *O. Lamarckiana* and *O. rubrinervis* in the latter instances, the first could not be called *lata*-like nor the latter *Lamarckiana*- or *rubrinervis*-like. In fact, only 2 of the 12 types were *lata*-like; namely, *O. lata* and *O. nanella lata*. On the other hand, *2 plants (2 types) were found in Cold Spring Harbor cultures of* O. Lamarckiana, *which were conspicuously* lata-*like in appearance, though differing from* O. lata *sufficiently to be regarded as distinct forms, and each had 16, and not 15, chromosomes.*

De Vries ('09, Vol. I., p. 224) gives a table showing the origin of new species from the type, *O. Lamarckiana.* From a first generation of 9 Lamarckianas he records 7 generations of descendants through *O. Lamarckiana* (1886–87 to 1899, inclusive) consisting of a total of 54,334 individuals, of which 834 were mutants, as follows:

TABLE I

| Species | *O. Lamarckiana* 14 | *O. nanella* 14 | *O. rubrinervis* 14 or $14^{+1}$ | *O. lata* 15 | *O. albida* 15 | *O. scintillans* Prob. 15 | *O. oblonga* 14 or 15 | *O. gigas* 28 |
|---|---|---|---|---|---|---|---|---|
| Number of individuals. . . | 53,500 | 158 | 32 | 229 | 56 | 8 | 350 | 1 |

Although the somatic chromosome number of *O. scintillans* is probably 15, the actual number is unknown, hence this type will be excluded from our calculations. If *oblonga* has 14 chromosomes, we see that approximately 20 percent of the total number of 15-chromosome forms were neither *O. lata* nor *lata*-like individuals. If *oblonga* has 15, then we see that almost 64 percent were neither *O. lata* nor *lata*-like forms. But de Vries states that the list is incomplete, as only the more important mutants were recorded; furthermore, since the records date from 1886, it is probable that even the common types were occasionally overlooked in the early years of the work; in fact he says (p. 229) that *albida* was passed by as a diseased form in 1888 and 1890. For these reasons the records of his 1895 *Lamarckiana* cultures are perhaps more significant (pp. 262–263). Of the total of 10,614 offspring of *O. Lamarckiana* he states that 614, or about 6 percent were mutants, "of which *O. albida* made up 2.5 %, *O. lata* 1.7 %, *O. nanella* 1.1 %, *O. oblonga* 0.7 % and the rest altogether 0.1 %." If we include *oblonga* and the unnamed mutants among the 15-chromosome forms, we see that the total number of *albida* plants alone equalled the total number of all other 15-chromosome mutants listed, including *O. lata.* We will assume that some of the unnamed types had 15 chromosomes and others 14 and that *oblonga* also had 14. If such were the case, the number of albidas not only exceeded the number of latas, but exceeded the combined number of 15-chromosome forms not listed as *O. albida.*

It is well known that a large percentage of Oenothera seeds fail to germinate in the short time commonly allowed them when sown in seed pans in January. De Vries ('15*a*) and Davis ('15*a*) have emphasized this fact recently and have suggested means of greatly increasing the percentage of germinations. ". . . we can not feel confident," Davis states ('15*b*), "that the records of any cultures of *Oenothera* so far reported are complete for their possible progeny. The percentages calculated for 'mutants' and the ratios of classes in breeding experiments can not be accepted as final in exact genetical work. We are not in a position even to guess what may be the changes of front when exact data become available." It is clear that future records of cultures, to be of value, must show that they are complete for their possible progeny.

*As a rule, seeds are obtained in greater abundance from 14-chromosome forms selfed, or pollinated by other 14-chromosome forms of the same, or different species, than from 14+-chromosome forms selfed, or pollinated by other 14+-chromosome plants of the same, or different species,—particularly if the 14+-chromosome individuals have more than 14, but fewer than 28, chromosomes.*

Beginning with the summer of 1908, I adopted the practice of counting all seeds sown; of planting seeds at spaced intervals in seed pans, and of recording the germinations. Only in a few instances have these precautions been neglected. The results have clearly shown that when seeds not more than one year old are sown in pans of sterilized soil in January and kept under ordinary greenhouse conditions, usually *larger percentages of germinations are secured within the first four or five months from seeds of 14-chromosome plants selfed, or pollinated by other 14-chromosome plants of the same, or different species, than from 14+-chromosome plants selfed, or pollinated by other 14+-chromosome plants of the same, or different species—particularly if the 14+-chromosome individuals have more than 14, but fewer than 28, chromosomes.* Hence it appears that *the number of seeds produced by a form and the ability of the seeds to germinate, at least within the time limits specified, are factors which are associated with the chromosome number of the plant, or numbers of the plants, producing them. The ability of a seed to germinate appears to depend, not wholly, but to a certain extent, upon the number of chromosomes which it bears, and, possibly, in accordance with Gates's suggestion* (15*a*, p. 194), *upon the compatibility, or incompatibility of the chromosomal combination which the number represents.* It also appears that *the ability of a seed to germinate is directly associated with its own chromosome number and only* *indirectly with that of its parents*, for the results derived from the Cold Spring Harbor and Louvain studies indicate that 14-chromosome offspring of 14+-chromosome forms may germinate as readily as 14-chromosome seeds of 14-chromosome forms.

In the discussions of this report and others to follow, due allowance will be made for the facts above mentioned. With reference to the relative percentages of the various types of mutants appearing in de Vries's cultures, as quoted, these may not represent the actual percentages as they would have appeared had all the viable seeds sown germinated, but they offer sufficiently satisfactory evidence to prove that many 15-chromosome offspring of 14-chromosome *Lamarckiana*, alone, have neither *lata*, *semilata*, nor *lata*-like, characters; furthermore, it is probable that the majority of these 15-chromosome mutants, whether *lata*-like or not, are products of 7 + 8 unions. However, if we believe that each 15-chromosome mutant is represented by a particular chromosomal combination, then we will agree that an occasional 6 + 9 union might produce the same combination as 7 + 8 and that the same type of mutant might result from the former as from the latter. This possibility may be illustrated very simply.

Throughout this paper and in future reports, when we wish to indicate difference in sex without designating the particular sex of either gamete, we shall employ small capitals in italics to represent the chromosomes of a gamete of one sex and the same, marked ′, to indicate the chromosomes of a gamete of the opposite sex; thus, (♂ or ♀) $A\,B\,C\,D\,E\,F\,G$ + (♂ or ♀) $A'\,B'\,C'\,D'\,E'\,F'\,G' = AA'\,BB'\,CC'\,DD'\,EE'\,FF'\,GG'$. When it shall be necessary to indicate the sex of gametes, the chromosomes of the female will be designated by lower case letters in italics, and those of the male by the same, marked ′; thus, ♀ $a\,b\,c\,d\,e\,f\,g$ + ♂ $a'\,b'\,c'\,d'\,e'\,f'\,g' = aa'\,bb'\,cc'\,dd'\,ee'\,ff'\,gg'$. Now, assuming that the regular female gamete of *O. Lamarckiana* contains $a\,b\,c\,d\,e\,f\,g$ chromosomes and the regular male $a'\,b'\,c'\,d'\,e'\,f'\,g'$; that the somatic cells of this form contain $aa'\,bb'\,cc'\,dd'\,ee'\,ff'\,gg'$ chromosomes; then $aa\,b\,c\,d\,e\,f\,g + a'\,b'\,c'\,d'\,e'\,f'\,g'$ might produce *O. lata* having $aaa'\,bb'\,cc'\,dd'\,ee'\,ff'\,gg'$ chromosomes. So also might $aa\,bb\,c\,d\,e\,f\,g + a' - c'\,d'\,e'\,f'\,g'$ produce *O. lata* having $aaa'\,bb\,cc'\,dd'\,ee'\,ff'\,gg'$ chromosomes. While it is possible that a 6-chromosome cell is incapable of functioning in union with one having 7 chromosomes, or fewer, but is capable of functioning in union with one having 8 or 8+ chromosomes, thereby producing a 14- or 14+-chromosome condition (Lutz, '12, p. 424), it cannot be assumed with safety that these common 15-chromosome *Lamarckiana* mutants result from the fusion of 6- and 9-chromosome gametes, except, possibly, in rare instances, for 5–9 distributions of heterotypic chromosomes doubtless occur still more rarely than 6–8, and a 9-chromosome cell would be expected to unite with a 7- far more frequently than with a 6- and to produce a 16-chromosome mutant; yet 16-chromosome offspring of *O. Lamarckiana* × *O. Lamarckiana* appear to be comparatively rare.

Gates ('09*a*, pp. 4–5) has pointed out that, owing to irregularities in chromosomal distribution, a germ cell might be formed containing two chromosomes of one pair and lacking both representatives of another pair. The number of chromosomes would therefore remain constant, he states, but such germ-cells would be entirely deficient in a particular kind of chromosome. He has further shown ('15*a*, p. 298) that if both members of one pair of chromosomes may pass to one pole of the heterotypic spindle, resulting in a 6–8 distribution of chromosomes, it is conceivable that both members of another pair might, on rare occasions, pass to the opposite poles at the same time. This would equip each daughter nucleus with 7 chromosomes, but not with the usual combination, ABCDEFG. Let us assume that this has occurred during male reduction and that two pollen grains bearing *a'a'– c' d' e' e' f' g'*, and two bearing *– bb' c'd'e' f'g'* chromosomes have been formed. Then should one of these male gametes, say of the first type, unite with a regular 7-chromosome female gamete, we should expect the 14-chromosome plant resulting to have *aa'a' b– cc' dd' ee' ff' gg'* chromosomes instead of the usual *aa' bb' cc' dd' ee' ff' gg'* combination. Gates and Miss Thomas suggested that "the variability of the *lata-semilata* series may depend upon the fact that the extra chromosome belongs to a different pair in different cases," and add: "since there are seven pairs of chromosomes, we should then expect seven more or less distinct *lata*-like types," but conclude that "there is at present no evidence that the plants having 15 chromosomes can be divided in this way."

If both members of any one of the seven pairs of chromosomes were capable of passing to one pole, while both members of any one of the remaining six were capable of passing to the opposite pole during male, as well as during female, reduction; if regular and irregular 7-chromosome male and female gametes were formed capable of uniting with each other and producing viable seeds, a large number of 14-chromosome combinations would be possible. If the common types of 15-chromosome mutant offspring of *O. Lamarckiana* could be limited to seven, one might assume that these are "half mutants" (borrowing de Vries's term, but applying it differently) resulting in each case from the union of a regular 7- with an 8-chromosome gamete, each of the latter entering into the union differing from every one of the remaining six with respect to the particular extra chromosome which it possesses. The union of any one of the many irregular 7-chromosome gametes with an 8- might produce one of the rarer types of 15-chromosome mutants and such a form might be regarded as a "whole mutant" (de Vries). The objections to these suggestions are obvious: irregular 7-chromosome distributions would be expected to occur more rarely than 6–8, and germ-cells resulting from the former would be expected to unite with regular 7-, producing 14-chromosome half mutants in the vast majority of cases, and to unite with cells having 8 chromosomes only in extremely rare instances. We would be obliged to conclude that the common 14-chromosome mutant offspring of *O. Lamarckiana* result from ♀ or ♂ regular (*Lamarckiana*) 7 + ♀ or ♂ irregular 7. If such were the case, one of these mutants, such as *O. nanella*, for example, could reproduce itself only by means of the union of dissimilar gametes,[19] probably of the same types as those which entered into the original combination. We have designated the *Lamarckiana* combination as $a\ b\ c\ d\ e\ f\ g + a'\ b'\ c'\ d'\ e'\ f'\ g' = aa'\ bb'\ cc'\ dd'\ ee'\ ff'\ gg'$; then if the mutant *nanella* resulted from $a\ b\ c\ d\ e\ f\ g + a'\ b'b' - d'\ e'\ f'\ g' = aa'\ bb'b'\ c-\ dd'\ ee'\ ff'\ gg'$, and if the male and female gametes produced by the mutant were each represented by the two types of gametes entering into the original combination, *O. Lamarckiana* × *O. nanella* should produce two types of offspring: $a\ b\ c\ d\ e\ f\ g + a'\ b'b' - d'\ e'\ f'\ g' = aa'\ bb'b'\ c-\ dd'\ ee'\ ff'\ gg'$, *O. nanella*, and $a\ b\ c\ d\ e\ f\ g + a'\ b'\ c'\ d'\ e'\ f'\ g' = aa'\ bb'\ cc'\ dd'\ ee'\ ff'\ gg'$, *O. Lamarckiana*. The same results should be secured from the reciprocal cross. As a matter of fact, de Vries ('13, p. 207) has shown that these are the results obtained from the two crosses; but how shall we explain the behavior of *O. nanella*, selfed? It is well known that this mutant breeds true, while on the basis of our previous assumptions, we should expect it to produce three types of offspring: (1)$a\ bb-d\ e\ f\ g + a'\ b'b'-d'\ e'\ f'\ g' = aa'\ bbb'b'-dd'\ ee'\ ff'\ gg'$, unlike both parents; (2) $a\ b\ c\ d\ e\ f\ g + a'\ b'b'-d'\ e'\ f'\ g' = aa'\ bb'b'\ c-\ dd'\ ee'\ ff'\ gg'$, *O.*

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[19] Unless apogamous development were possible.

*nanella.* The reverse combination should also reproduce the parental type. (3) $a\,b\,c\,d\,e\,f\,g + a'\,b'\,c'\,d'\,e'\,f'\,g' = aa'\,bb'\,cc'\,ee'\,ff'\,gg'$, *O. Lamarckiana.* The first combination might be excused on the pretext of incompatibility, but this would hardly be sufficient to account for the absence of *O. Lamarckiana* from among the offspring of selfed *nanella.* Our difficulties are not lessened, as a little figuring will show, by assuming that two types of gametes are produced by one sex, and only one by the other, such as ♀ $a\,bb-d\,e\,f\,g$ and $a\,b\,c\,d\,e\,f\,g$ + ♂ $a'\,b'b'-d'\,e'\,f'\,g'$ or ♂ $a'\,b'\,c'\,d'\,e'\,f'\,g'$; or by assuming that all of the female gametes are of one type and all of the male of another type. Let us then consider the problem from another viewpoint. We may assume that these irregular 7-chromosome mutant gametes of *O. Lamarckiana*, notwithstanding their numerous opportunities to unite with regular (*Lamarckiana*) 7-, are incapable of doing so, because of incompatibility, and that a gamete of this type can unite only with another of its kind: $a\,bb - d\,e\,f\,g + a'\,b'b' - d'\,e'\,f'\,g' = aa'\,bbb'b' - dd'\,ee'\,ff'\,gg'$, *O. nanella;* also that the mutant produces male and female gametes of the same, single type. Our difficulties would still be with us, for *O. nanella* × *O. Lamarckiana*, and the reciprocal, would result in a new type (the same in both instances) quite unlike either parent. Furthermore, if the original irregular 7-chromosome mutant gamete produced by *O. Lamarckiana* were incapable of uniting with a regular 7-*Lamarckiana* gamete in *O. Lamarckiana* selfed, we would expect the two to be unable to unite in the crosses, yet we know that seed and offspring are readily secured from both. Even should we assume that the *nanella* group $aa'\,bbb'b'-dd'\,ee'\,ff'\,gg'$, resulting from the union of identical gametes, produces female gametes of one type and male of another, such as $a\,bbb-d-f\,g$ and $a'\,b'-d'\,e'e'\,f'\,g'$, our difficulties would not disappear. It seems impossible, on a chromosomal basis, to find an explanation for the fact that *nanella* and *Lamarckiana*, when selfed, produce only *nanella* in the first case, and only *Lamarckiana* in the second (barring rare exceptions), but that *O. nanella* × *O. Lamarckiana* and the reciprocal, produce both parental types in each case. Truly he who attempts to explain mutation on a strictly chromosomal basis finds his pathway beset with many obstacles.

We do not know whether 15-chromosome mutant offspring of 14-chromosome *O. Lamarckiana* result from unions of ♀7 with ♂8, or ♀8 with ♂7, or from both combinations; since there is considerable evidence to indicate that functional 8-chromosome cells of one sex only are produced by certain 15-chromosome individuals, and that these, in many forms, are female, it is possible that the functional 8-, perhaps even all functional 7+-chromosome germ-cells produced by *O. Lamarckiana* and certain 14-chromosome mutant derivatives, are female.[20] More attention has been directed to the study of male than female reduction in various forms. Gates ('10, reported in 1907) and Davis ('11) each recorded 6–8 distributions of male heterotypic chromosomes in *O. Lamarckiana*, but as Davis remarks (p. 952) "we do not know whether or not fertile pollen-grains may be formed with chromosomes in a greater or less number than the normal."[21] Gates and Miss Thomas ('14) found the expected 7–8 distributions of heterotypic chromosomes in the pollen mother cells of *O. lata;* we know that 8-chromosome female gametes are produced by this form, yet we shall see that it appears that very few, if any, 8-chromosome male gametes, capable of functioning, are formed; nor is the presence of the two 16-chromosome plants in the C.S.H. culture of *O. Lamarckiana* positive proof of the production of both male and female 8-chromosome germ-cells, since we do not know whether these individuals arose from 8 + 8, or 9 + 7 unions. It is quite certain, however, that 7+-chromosome cells of one sex or the other, if not of both, are formed occasionally, since 15-chromosome mutants are quite common.

We may summarize our conclusions, therefore, as follows:

(*a*) *15-chromosome mutant offspring of 14-chromosome forms are not invariably distinguished by the somatic characters of* O. lata, O. semilata *or* lata-*like forms.*

(*b*) Lata-*like forms, and those combining certain* lata *characters with others not distinctive of* O. lata, *are not invariably characterized by 15 chromosomes.*

Thus far we have considered only (*a*) whether when a meiotic irregularity in a 14-chromosome form results in the production of a

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[20] This statement merely expresses a possibility and not the writer's established convictions. If 7+-chromosome male gametes, capable of functioning, are never produced by *O. Lamarckiana*, then we must concede that *O. gigas* de Vries arose in some one of the various ways suggested by Gates (and recent evidence tends to strengthen, rather than weaken, Gates's arguments in support of this conclusion) and that it was not the product of the union of two 14-chromosome gametes, as maintained by Stomps and Lutz.

[21] By *O. Lamarckiana.*

15-chromosome offspring, such an individual will have the leaves and habit of *O. lata* or *O. semilata* invariably, or even in the majority of cases (Gates, '13) and (*b*) whether the frequency of the occurrence of an irregular distribution of the chromosomes of 14-chromosome plants into 6–8 groups may determine the frequency with which *lata*-like mutants will appear (Gates and Miss Thomas, '14). We have yet to consider (*c*) whether when *O. lata* is crossed with its 14-chromosome parent, or is selfed, the percentage in which *O. lata* appears among the offspring is indicative of the number of 9- and 7-chromosome germ-cells which function (Gates and Miss Thomas). This question will be treated under the following head.

### 3. *Are 15-chromosome Forms Inconstant?*

Of the twenty-one 15-chromosome mutants which Gates and Miss Thomas reported, three were identified as *O. semilata*, one as *lata* to *semilata* and two as *semilata* to *lata*. Referring to de Vries's cultures of *O. lata* and *O. semilata* they say (p. 527): "*Oe. lata* was classed by him as an inconstant species, but *semilata* was incorrectly classed as constant. They are both obviously inconstant, however, and *the presence of the odd chromosome shows why this must be so.*" (Italics not employed in the original.) Gates ('15*a*, pp. 111–112) has since found that the mutant which he described as *semilata* is not the same as de Vries's mutant of this name, but has decided to retain the name for the form reported by Gates and Miss Thomas, since the Amsterdam type is extinct. Therefore, when it becomes necessary to distinguish between these two types, we shall designate them as *O. semilata* de Vries and *O. semilata* Gates, respectively.

Gates and Miss Thomas's statement raises the question, Does the presence of the odd or extra chromosome necessarily render a form inconstant? Are 15-chromosome forms never constant?

Since 15-chromosome forms produce, as a rule, no pollen, very little, or a moderate amount containing a high percentage of bad grains;[22] since seeds are obtained from selfed forms with difficulty, and when secured, usually a much lower percentage of these than of the seeds derived from 14-chromosome forms succeed in germinating in the short time commonly allowed them, their constancy has not been tested on an extensive scale. Inasmuch as we know that in certain cases but one small culture of offspring from these plants, selfed, has been grown, and have reason to believe that only one or two, containing but very few offspring, have been grown from others, and since it is probable that the offspring derived from these forms, as recorded by various workers, do not represent the whole of the possible progeny in any case, *i. e.*, do not represent all that would have been obtained had means been employed to secure the germination of every seed capable of germinating—it is clear that the evidence upon which we would like to base our conclusions is not wholly reliable. This fact should be borne in mind throughout the discussions which follow. Nevertheless, the evidence as it now stands is not devoid of significance.

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[22] Plants having more than 14, but fewer than 28, chromosomes are much more inclined to be male- than female-sterile. Just why this is so, is not yet clear.

*O. lata* (15) produces, as we shall see, *O. Lamarckiana*, *O. lata*[23] and a certain percentage of mutants,—the number of Lamarckianas greatly exceeding the number of latas in the cultures grown by MacDougal and de Vries. The behavior of *sublinearis*, if a 15-chromosome form, appears to be similar to that of *O. lata*, since the 31 offspring which de Vries obtained from *sublinearis*, selfed ('09, Vol. I., p. 401) were classified by him as follows: 19 *Lamarckiana*, 3 *sublinearis*, 1 *lata*, 1 *nanella*, 1 *albida*, 3 *subovata*, 2 *oblonga* and 1 *gigas*.[24] Here again we see that the number of Lamarckianas greatly exceeded the number of forms which reproduced the characters of the mutant parent. *O. bipartita* (15), selfed, produced *O. Lamarckiana*, *O. bipartita*, a few forms resembling the parent in most ways but having fewer flowers with cleft petals and extra-lobed stigmas than is common, and a few mutants. Here, also, a higher percentage of Lamarckianas than of bipartitas was obtained in the time allowed for the germination of the seeds, probably about 4 months.

As previously stated, the number of chromosomes present in *O. scintillans* is unknown, but it is probable that it is 15. This form, when selfed, according to de Vries ('13, p. 257), produces a variable number of *scintillans;* sometimes 35–40 percent or less and again as high as

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[23] Bartlett ('15*a*, p. 103) calls attention to the similarity in the behavior of *O. lata* and *O. stenomeres* mut. *lasiopetala*. From the latter form, selfed, he obtained 60 percent *stenomeres* and 40 percent *lasiopetala*. Mr. Arzberger has counted 14 chromosomes in *O. stenomeres*; the chromosome number of *O. lasiopetala* has not yet been announced, but it is probably 15.

[24] De Vries has since concluded ('12, p. 34) that this plant and the other identified as *O. gigas* in 1899 ('09, Vol. I., p. 327) were probably triploid, and not tetraploid, forms.

70–80 percent of the total number of offspring reproduce the characters of the mutant parent. The remainder are, for the most part, *O. Lamarckiana*, but with a considerable number of *O. oblonga* ("oft bis 20%") and a few other mutants.

*O. semilata* Gates (15), is an inconstant form, as Gates and Miss Thomas ('14, p. 532) and Gates ('15*a*, pp. 114–115) have shown, producing *O. Lamarckiana*, *O. semilata* Gates, a few *O. lata* which may be classed as mutants and (p. 114) others "forming a continuous series running to *Lamarckiana*."

*O. elliptica*, having 15(?), chromosomes, reverts almost entirely to *Lamarckiana*, according to de Vries ('09, Vol. I., pp. 397–398). From one 1895 mutant, selfed, he obtained "some hundred of seedlings," all of which proved to be ordinary *Lamarckiana*. From a second mutant of the same year 500 offspring were secured, 1 of which was *elliptica*, and the remainder *Lamarckiana*. A third 1895 mutant "gave rise to 27 seedlings not one of which was an *elliptica*." From an 1896 mutant he obtained 32 offspring, 5 of which were *elliptica* and the remainder *Lamarckiana;* from an 1899 mutant he secured about 100 offspring, all of which were *O. Lamarckiana*.

*O. lata rubricalyx*, in which Gates and Miss Thomas counted 15 chromosomes, when selfed, according to Gates ('15*a*, p. 288), produced a nearly uniform lot of offspring (44 plants), "all having the red pigmentation of *rubricalyx*, but were intermediate between *rubricalyx* and *grandiflora* in foliage and buds. . . . The plants which were examined had 14 chromosomes, as was doubtless the case with all of them." No *lata rubricalyx* plants were found among the offspring.

While all of the above forms are clearly inconstant, de Vries's researches indicate that a 15-chromosome form may breed perfectly true. He selected 5 biennial *albida* plants ('09, Vol. I, p. 229) in 1897 and grew a second generation consisting of 86 individuals in 1898 and a third, consisting of 36, in 1899. "Both generations," he adds, "were absolutely constant and exhibited no signs of reversion."

If *O. oblonga* be a 15-chromosome form, it indicates even more strongly (because of the larger number of offspring obtained) that a 15-chromosome form may be constant. During a period of over 13 years, de Vries (pp. 346–348; also, '13, p. 315) selfed a number of *oblonga* mutants and obtained a total of 2,919 offspring, all of which, with the exception of 11 mutants (7 *rubrinervis*, 3 *albida*, 1 *elliptica*) were *oblonga*.

Certain somatic characters of many mutant offspring of *O. Lamarckiana* × *O. Lamarckiana* and of *O. Lamarckiana*, selfed, indicate that *a very large percentage of the mutant offspring of* O. Lamarckiana *have 15 chromosomes and that a larger number of 15- than of 14-chromosome mutant offspring are produced by this form. Not only does there appear to be a larger number of distinct types of 15- than of 14-chromosome mutants, but a higher percentage of 15- than of 14-chromosome mutant individuals produced by* O. Lamarckiana. Many of the mutant offspring of *O. Lamarckiana* never have been brought to flower; furthermore, new forms are appearing each year. It will be necessary to determine the somatic chromosome numbers of a large percentage of the mutant types produced by *O. Lamarckiana,* to bring the 15-chromosome forms to flower, to self flowers on all parts of the plants, to adopt methods which will secure the germination of all viable seeds, and to grow large numbers of offspring,—in order to ascertain whether 15-chromosome forms are more commonly inconstant than constant. The majority of the 15-chromosome forms whose constancy we have considered have produced very few offspring, yet we may safely assert that the evidence available at present indicates that *most 14-chromosome forms are constant and most 15-chromosome forms inconstant.* Furthermore, although our present knowledge of the behavior of 14+-chromosome forms is very limited, largely owing to the infrequency with which good pollen is produced by such forms, it may be stated that the evidence available at present indicates that *inconstancy is commonly associated with the 14+-chromosome condition.* It seems, however, that forms having twice 14 chromosomes are more likely to be constant—in the same sense that *O. gigas* de Vries is constant—than those having more than 14, but fewer than 28, chromosomes.

### 4. *Factors Determining the Constancy or Inconstancy of 15-Chromosome Forms.*

De Vries obtained the same results from *O. scintillans* selfed, as from *O. scintillans* × *O. Lamarckiana* (pp. 257–262); also the same results from selfed hybrid *lata,* descended through *O. lata* × *O. Lamarckiana* from *O. lata* × *O. semilata,* as from *O. lata* × *O. Lamarckiana* ('09, Vol. I., pp. 240, 360; '13, pp. 244–257). This led him to conclude that female gametes of *O. scintillans* and this hybrid *lata* do not bear the same hereditary characters as the male gametes of these forms; that the characters of the mutant, in the first case, and of the hybrid (which are the same as those of mutant *O. Lamarckiana lata*), in the second, are transferred to the offspring through the egg cells, and not through the pollen; that the pollen, in each case, behaves precisely as the pollen of pure *Lamarckiana* (pp. 257, 258, 262, 272, 273, 323).

At the time of the publication of "Gruppenweise Artbildung", *O. lata* was popularly supposed to be the only 15-chromosome mutant produced by *O. Lamarckiana* or other forms, hence de Vries has discussed these very important results without reference to the chromosome numbers of the plants in question. However, since a number of forms are now known to have 15 chromosomes, their behavior may be further considered in the light of this fact.

Bartlett ('15*a*, p. 103), discussing the behavior of selfed *O. lata* and *O. stenomeres* mut. *lasiopetala*, concludes, in agreement with de Vries, that "it appears that the good pollen grains of *Oe. lata* are genetically the same as those of *Oe. Lamarckiana*, and do not carry the *lata*-characters." "Thus," he states, "it appears that there is a class of mutations of which the eggs are of two kinds; one kind carries the characters of the parent species, the other kind the characters of the mutation. The pollen grains, however, appear to be of one kind only, and to carry the characters of the parent species." He says "we must assume that the male 8-gametes are eliminated" and asks if it is not possible "that the male gametes which carry the characters of the mutation are eliminated because of some physiological defect?" "*Oe. lata*," he states, "produces two classes of gametes, with 8 and 7 chromosomes, respectively. If two 7-gametes fuse, we have *Oe. Lamarckiana;* if a 7-gamete (presumably male) fuses with an 8-gamete (presumably always female) we have *Oe. lata*." We shall see that the evidence indicates such are the usual, though not the invariable, results.

MacDougal ('07) obtained 94 offspring from selfed *O. lata* which were identified as follows: 10 *O. lata*, 80 *O. Lamarckiana*, 1 *O. albida* and 3 *O. oblonga*. *Albida* has 15 chromosomes and *oblonga* 14 or 15. De Vries ('13, p. 256) obtained 442 offspring from a hybrid *lata*, selfed, 33 percent of which were *O. lata* and 4 percent mutants. The remainder were, doubtless, *O. Lamarckiana*. It is probable that several types of 15-, and one or more 14-chromosome forms were included among these 17 or 18 mutants.

In 1908 3 mutant *lata* offspring of *O. Lamarckiana* were selfed at Cold Spring Harbor. A total of 360 seeds were obtained and these were planted at spaced intervals in pans of sterilized soil, December 11 of the same year. 129 germinations resulted; 2 plants died unidentified as seedlings and a third, identified as *O. Lamarckiana*, died later. The remaining 126 were transferred to the garden May 12, 1909. One *lata* from each of the three 1909 cultures was then selfed and the 259 seeds obtained were sown in the same manner as those of the preceding season, March 7, 1910. 99 germinations resulted; all of the seedlings survived and all of the young plants were transferred to the experimental garden May 16, following.

Of these 226 plants, 109 (approximately 50 percent) were clearly identified as *O. lata*, 8 as *O. lata* (?), 57 as *O. Lamarckiana* (approximately 25 percent) and 4 as *O. Lamarckiana* (?). The chromosome numbers of the plants in the second and fourth groups are unknown. In addition to the foregoing there were 7 distinct types of 15-chromosome mutants (23 individuals) which could not be classified either as *O. lata* or as *lata*-like forms. Still other mutant types, whose chromosome numbers were unknown, were believed to be 15-chromosome forms. In addition to the 57 Lamarckianas there were 3 types (4 individuals) of 14-chromosome mutants, quite unlike *O. Lamarckiana*. These are believed to represent approximately the total number of 14-chromosome forms produced. 196 of the 226 plants grown represented types whose chromosome numbers are now known, and but one of the 196 had 16 chromosomes.[25] De Vries's mutants were not classified, but it is quite clear that no one of the 94 offspring which MacDougal obtained from selfed *lata* had 16 chromosomes. We do not know how many of MacDougal's and de Vries's seeds failed to germinate, but we have seen that 63 percent of the Cold Spring Harbor seeds sown failed to germinate in the few months allowed them, hence we do not know what would have been the relative percentages of 14-, 15- and 16-chromosome forms, had all the viable seeds sown germinated.

In connection with these studies of selfed latas, the results obtained from crossing one of these 1908 mutants with *O. Lamarckiana* will be of interest. In 1908 I pollinated *O. lata*, mutant No. 3500, with *O. Lamarckiana*, No. 3814, and covered the stigmas of the latter plant with small quantities of pollen obtained from the former. 15 chromosomes were counted in the somatic cells of No. 3500 and 14 in those of No. 3814. 320 seeds from *O. lata* × *O. Lamarckiana* were planted at spaced intervals in seed pans, December 12, 1908; 49 of this number germinated previous to the time of transplanting in May. Four of the young plants died as seedlings and the remainder were classified as follows:

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[25] In addition to the 14-, 15- and 16-chromosome offspring referred to, one 21- and one 22-chromosome mutant were produced, as previously reported (Lutz, '12). The 226 offspring of these six selfed latas will be carefully tabulated and fully described in a later report.

TABLE II

*O. lata* No. 3500 × *O. Lamarckiana* No. 3814

| | *O. Lamarckiana* | *O. aberrans* | *O. lata* | *O. albida* | Type 5432 | Totals |
|---|---|---|---|---|---|---|
| 14 chromosomes...... | 15 | .... | .... | .... | .... | 15 |
| $14^{+1}$ " ...... | .... | 1 | .... | .... | .... | 1 |
| 15 " ...... | .... | .... | 27 | 1 | .... | 28 |
| ? " ...... | .... | .... | .... | .... | 1 | 1 |

On December 11, 1908, the same number of seeds from the second cross (*O. Lamarckiana* × *O. lata*) were planted in the same manner as the above. Only 18 germinated; therefore, on February 1, 1909, 119 seeds from the same capsules as the preceding were planted and 58 seedlings obtained previous to the middle of May. The 76 plants derived from this cross were classified as follows:

TABLE III

*O. Lamarckiana* No. 3814 × *O. lata* No. 3500

| | *O. Lamarckiana* | *O. nanella* | Type 3514 (modified *rubrinervis?*) | *O. lata* | *O. bipartita* (?)[26] | Totals |
|---|---|---|---|---|---|---|
| 14 chromosomes...... | 63 | 1 | 9 | .... | .... | 73 |
| 15 " ...... | .... | .... | .... | 1 | 2 | 3 |

From these tables we see that in the time allowed for germination, almost twice as many 15- as 14-chromosome offspring were derived from *O. lata* × *O. Lamarckiana*, while only 3, possibly only 1, of the 76 plants derived from *O. Lamarckiana* × *O. lata* had 15 chromosomes. Since one or more 15-chromosome mutants usually are found in *Lamarckiana* cultures of this size, it is probable that the 15-chromosome offspring of *O. Lamarckiana* × *O. lata* resulted from ♀8 + ♂7 and possible (providing 8-chromosome gametes are formed by *O. Lamarckiana*) that one or two of those derived from the reciprocal cross were products of ♀7 + ♂8 unions. Notwithstanding the fact that 85 percent of the *lata* × *Lamarckiana*, and 83 percent of the *Lamarckiana* × *lata*, seeds failed to germinate in the time allowed them—approximately the same percentage of failures in both cases—15-chromosome forms appeared in considerable numbers among the offspring of the first cross, but were almost entirely absent from the second culture. However, we do not know what the percentages of 14- and 15-chromosome offspring would have been had all the seeds of each cross germinated.

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[26] The identification of these supposed bipartitas was based upon the characters of the greenhouse rosettes, as the plants were not transferred to the garden.

Bearing in mind that we do not know "what may be the changes of front when exact data become available," it may be said that the C.S.H. cultures of mutant *O. Lamarckiana lata* selfed and crossed both ways with *O. Lamarckiana* confirm, in the main, the earlier statements by de Vries and Bartlett and point to the following conclusions regarding this mutant: (*a*) *Lata* characters are transmitted through a portion of the egg cells, and not, except possibly in rare instances, through the pollen of this form. (*b*) 8- and 7-chromosome female gametes, capable of functioning, but as a rule, only 7-chromosome male gametes, capable of functioning, are produced by *O. lata*.[27] The majority of the 8-chromosome female gametes (probably not all) are bearers of *lata* characters, while the majority of the male and female 7-chromosome gametes (probably not all) are bearers of *Lamarckiana* characters. (*c*) It now appears that when offspring result from 8 + 7 and 7 + 7 unions, the majority of the former have *lata*, or *lata*-like characters, and the majority of the latter *Lamarckiana* characters, but, as in the case of *O. Lamarckiana*, selfed, it is not safe to assume that such are the invariable results, since it is probable that at least a portion of the 15- and 14-chromosome offspring derived from *O. lata* selfed, *O. Lamarckiana*, selfed, and *O. lata* × *O. Lamarckiana* which cannot be classified as *O. lata* and *O. Lamarckiana*, are products of 8 + 7 and 7 + 7 unions, respectively. As in the case of *O. Lamarckiana*, *O. albida* is one of the common mutant offspring of *O. lata*, selfed, and of *O. lata* × *O. Lamarckiana* and it seems quite probable that this form results from 8 + 7 unions.

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[27] Fourteen- and fifteen-chromosome mutants, particularly the latter, are found in practically all fair-sized cultures of *O. lata* × *O. Lamarckiana*. No statement can be made concerning the appearance of these forms in cultures of the reciprocal cross, since only one has been reported thus far.

While, as we have seen, de Vries has shown that *O. scintillans*, when selfed or pollinated by *O. Lamarckiana*, behaves in much the same way as *O. lata* under similar conditions, statements concerning the chromosomal combinations resulting from these operations must be wholly speculative since the numbers of chromosomes present in *O. scintillans* and its *oblonga* offspring are unknown. However, if *scintillans* has 15, as is probable, there is much evidence to indicate that 7- and 8-chromosome female gametes, capable of functioning, and, as a rule, only 7-chromosome male gametes, capable of functioning, are produced by this form,[28] whether *oblonga* has 14 or 15 chromosomes. That only 7-chromosome male gametes are produced which behave in every way like the 7-chromosome male gametes of *O. Lamarckiana* is clearly indicated by the fact that while *O. scintillans*, selfed, and *O. scintillans* × *O. Lamarckiana* produce *O. scintillans*, *O. Lamarckiana* and *O. oblonga*, *O. Lamarckiana* × *O. scintillans* yields 100 percent *O. Lamarckiana* (de Vries, '13). A noteworthy peculiarity in the behavior of *O. scintillans* is the relatively large number of offspring of one type derived from the mutant, selfed, and pollinated by *O. Lamarckiana*, which display neither the characters of *O. scintillans* nor of *O. Lamarckiana*, but of the mutant, *O. oblonga*. This indicates either that a relatively large percentage of the offspring resulting from 8 + 7 unions fail to reproduce the characters of the mutant parent, or that a relatively large percentage of those derived from 7 + 7 unions fail to display the characters of *O. Lamarckiana*.

The behavior of *O. bipartita* and of *O. sublinearis* (if the latter has 15 chromosomes, and it is probable that it has) indicates that all, or nearly all, of the gametes of one sex which are capable of functioning, contain 7 chromosomes, while a portion of those of the other sex contain 7 and the remainder 8. The same may be said of *O. semilata* Gates if the offspring which Gates refers to as "forming a continuous series running to *Lamarckiana*" have either 14 or 15 chromosomes.[29]

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[28] In the case of *O. lata* and other forms to be discussed in this report, it will be understood that the writer does not exclude the possibility of other gametes being formed occasionally in addition to those enumerated—gametes having fewer than 7, or more than 7 or 8 chromosomes. For instance, as earlier stated, it is conceivable that 6-chromosome gametes may function in union with 8- or 8+-. It is possible that 9-chromosome gametes, capable of functioning, may be produced occasionally by 14- and 15-chromosome forms, particularly the latter, and we know that there is much evidence to show that 14-chromosome gametes are sometimes produced by 14-chromosome forms (possibly also by 15-) and 15-chromosome gametes by 15-chromosome forms.

*O. stenomeres* mut. *lasiopetala*, as Bartlett ('15*a*) has pointed out, resembles *O. Lamarckiana* mut. *lata* in its behavior, with, of course, this exception: the 14-chromosome offspring of the former bear the characters of *O. stenomeres*, and not of *O. Lamarckiana.* In each case, however, the offspring bear the characters of the 14-chromosome form which produced their mutant parent. Furthermore, as in the case of *O. lata*, a portion of the offspring (presumably having 15 chromosomes) reproduce the characters of the mutant parent.

The behavior of *O. elliptica*, if a 15-chromosome form, indicates that all of the gametes of one sex, capable of functioning, have 7 chromosomes, while the majority of those of the other sex which are capable of functioning have 7 chromosomes, and only a very few, 8.

The behavior of *O. nanella lata* indicates that only 7-chromosome female gametes are produced by this form since de Vries ('09, Vol. I., p. 374) found that *O. nanella lata* × *O. nanella* "gave rise to ordinary *nanella* only." From *O. lata* × *O. Lamarckiana* de Vries ('13, p. 257) obtained two dwarfs through mutation. "Der eine hatte nebenbei die Merkmale der *Lamarckiana*, der andere diejenigen der *Lata.* Beide hatten Pollen, und wurden damit rein befruchtet. . . . Die letztere gab zwar auch nur Zwerge . . . , spaltete sich aber in bezug auf die *Lata*-Merkmale in 9 *Lata*-Zwerge und 18 gewöhnliche Zwerge, . . . ". The latter, upon self-fertilization, proved constant, but the *lata* dwarfs behaved in the same manner as the parent, when selfed.[30] If this *lata* dwarf is the same form as de Vries's *O. nanella lata*, then the available evidence indicates that all of the female cells of this mutant which are capable of functioning contain 7 chromosomes, while the majority of the male contain 7 and a smaller number 8.[31] Little or no consideration should be given to this evidence, however, since we do not know that the two mutants combining *nanella-lata* characters were duplicate types; furthermore, we have no assurance that a sufficient number of offspring of *O. nanella lata* × *O. nanella* were grown to prove that *O. nanella* only, invariably results from this cross; and finally, since only 27 offspring were derived from the later mutant, selfed, it is clear that we are not justified in formulating definite conclusions concerning its behavior.

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[29] This condition was earlier indicated by Bartlett ('15*a*, p. 103) in the statement that "*Oe. scintillans* acts like *Oe. lata* in every way."

[30] *O. rubrinervis lata*, which appeared in Schouten's 1906 culture of *O. rubrinervis* (Schouten, '08), suggests a 15-chromosome condition, as Gates ('15) has stated, but since the chromosome number of this plant is unknown and that of the parental type unestablished, the behavior of this mutant will not be discussed at present.

[31] The behavior of *O. oblonga*, if a 15-chromosome form, is somewhat contradictory and will not be discussed here.

The behavior of *O. lata rubricalyx* is somewhat unique. If all of the offspring of the mutant, selfed, had 14 chromosomes, as Gates thinks probable, this fact would indicate that all of the male and female cells produced which were capable of functioning, had 7 chromosomes. This is further indicated by the fact that although Gates crossed the mutant both ways with several other forms, "the offspring (few in number) which developed proved to be all of 14-chromosome types." He does not state whether the several forms employed in these crosses were 14- or 15-chromosome plants, but the results indicate that only ♀7 + ♂7 unions occurred in every case, or at least that only seeds resulting from these unions germinated in the time allowed them. Of especial interest is the fact that the 14-chromosome offspring of this plant were intermediate between *rubricalyx* and *grandiflora* (the grandparents). Would the mutant behave differently if produced by *rubricalyx*, selfed? Is this precise type ever produced by *rubricalyx?*

In the case of *O. albida*, all of the cells of one sex appear to contain 7 chromosomes and all of the other 8, since de Vries obtained *albida* offspring only from this form, selfed.

Thus, in addition to *O. lata*, the records show that a certain number —commonly more than half—of the offspring derived from selfed *O. bipartita*, *O. scintillans*, *O. sublinearis* and almost all of those obtained from selfed *elliptica* (the evidence is not clear in regard to *O. semilata* Gates) were 14-chromosome plants and that all of them, or all but a few mutants (providing the *oblonga* offspring of *O. scintillans* had 15 chromosomes), were *O. Lamarckiana.*[32] Hence the evidence as it now stands indicates that all but relatively few of the 7-chromosome male and female gametes of these plants (providing *scintillans* and *sublinearis* are 15-chromosome forms) are bearers of *Lamarckiana* characters[33] and that the mutant characters of the 15-chromosome parent in each case are transmitted to the offspring through the 8-chromosome gametes. In cases with which we are familiar, the 8-chromosome cells appear to be produced wholly, or almost wholly, by one of the two sexes; this is clearly female in certain cases, but we may find that these cells are male in others.[34] Without considering the question of whether these forms, when given off as *Lamarckiana* mutants are "half mutants" (de Vries), it is clear that a *Lamarckiana* offspring is produced by selfed 15-chromosome mutant derivatives of *O. Lamarckiana* when two gametes, each bearing *Lamarckiana* characters, and, possibly, the chromosomal combination peculiar to these gametes, unite and produce a seed capable of germinating. Bartlett ('15*a*), after stating that certain mutants appear to produce two kinds of eggs, one carrying the characters of the mutant producing them and the other the characters of the parent species, while the pollen grains appear to be of one kind only and to carry the characters of the parent species, adds: "If so, *Oe. lata* might be supposed to originate by the union of a *lata*-egg (itself constituting the true mutation) with a *Lamarckiana*-sperm." Accepting Bartlett's suggestion, it may be said of all 15-chromosome mutant derivatives of *O. Lamarckiana* which, when selfed, produce two types of offspring, one duplicating the characters of the mutant parent and the other those of *O. Lamarckiana*, that an offspring of the first type is obtained from these forms, selfed, when an 8-chromosome gamete bearing the characters of the mutant parent, and, possibly, the chromosomal combination peculiar to these gametes, unites with a 7-chromosome gamete bearing *Lamarckiana* characters, and possibly, the chromosomal combination peculiar to *Lamarckiana* gametes, and produces a seed capable of germinating. If we consider this matter on a strictly chromosomal basis, we will concede, of course, that 9 + 6, or any other union which produces the same chromosomal combination as the ordinary 8 + 7, might result in an offspring which would duplicate the vegetative characters of the 15-chromosome parent. However, *since 14-chromosome offspring of 15-chromosome plants and 15-chromosome offspring of 14-*

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[32] It is probable that the list of forms which produce large numbers of *O. Lamarckiana* when selfed, might be extended to include many other direct and indirect 15-chromosome mutant derivatives of *O. Lamarckiana*, but not all; *O. nanella lata* and *O. rubrinervis lata* may be suggested, among others, as probable exceptions.

[33] The evidence indicates that all of the 7-chromosome gametes of one sex produced by *O. elliptica* and all but comparatively few of the opposite sex, which are

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capable of functioning, are bearers of *Lamarckiana* characters. It is probable that 7-chromosome *Lamarckiana* gametes (of one sex) are produced by *O. albida*, but experimental evidence has not indicated the facts in the case.

[34] Doubtless these assertions, and the conclusions regarding *O. lata* under the heads of (*a*), (*b*) and (*c*) on page 87 would be equally applicable to many other 15-chromosome mutant derivatives of *O. Lamarckiana*, if the names of these mutants, in the latter case, were substituted for that of *O. lata*.

*chromosome plants never duplicate the vegetative characters of their parents, it is clear that 8 + 8* (lata *8* + lata *8, for example) could not produce an individual having the same vegetative characters as the 15-chromosome parent.*[35]

In view of the fact that when certain 15-chromosome forms are selfed, the parental mutant type appears to be reproduced by 8 + 7, and never by 8 + 8, unions, one may ask whether we are not justified in asserting that the 7-chromosome cells are as truly transmitters of the mutant characters as the 8-; it seems that they are not, for the 22-chromosome offspring of *O. lata* × *O. gigas*, which presumably result from ♀8 + ♂14 unions, suggest *lata-gigas* characters, while 21-chromosome hybrids, which doubtless result from ♀7 + ♂14 unions, suggest *Lamarckiana-gigas* combinations. Since the latter bear no trace of *lata* characters, it is clear that these are transmitted through the 8-, and not through the 7-chromosome gametes.

If 7- and 8-chromosome male and female gametes were produced in equal numbers, all capable of functioning in union with 7- and 8-chromosome cells of the opposite sex, we would expect a selfed 15-chromosome form to produce 14-, 15- and 16-chromosome offspring in the ratio of 1:2:1. How, then, shall we explain the fact that the number of 14-chromosome offspring produced usually (not invariably, as we have seen) exceeds the number of 15-, while 16-chromosome forms are almost unknown in such cultures? How shall we explain the fact that $F_1$ cultures derived from 15-chromosome forms pollinated by 14- usually contain many more 14- than 15-chromosome plants?[36]

1. In the first place, it will be recalled that no evidence has been brought forward to show that 8-chromosome male gametes, capable

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[35] It is quite probable, however, that *lata*-like mutants may result from *lata* 8 + *lata* 8.

[36] After the manuscript for this report had left the writer's hands, an important contribution from de Vries appeared, entitled "New dimorphic mutants of the Oenotheras" (Bot. Gaz. **62**: 249–280, Oct., 1916). In this report de Vries has shown that *O. cana*, which is probably a 15-chromosome form, produces *O. cana* and *O. Lamarckiana* when selfed, but that a larger percentage of the offspring duplicate the characters of the mutant parent when a biennial, than when an annual, plant is employed. This fact demonstrates, as he states, that the behavior of *O. cana* is largely dependent upon the vigor of the individual employed. De Vries believes that this is true of other dimorphic mutants, since he had earlier demonstrated this difference in the behavior of annual and biennal *scintillans*. The bearing of these important facts upon the statements which are included under the heads of 1, 2 and 3 above, will be discussed in a later publication.

of functioning, are produced by 15-chromosome forms. So far as has been observed, the male gametes appear to be, with rare exceptions, exclusively 7-. It is possible that the embryo-sac is more frequently differentiated from a 7- than from an 8-chromosome group, and that more 7- than 8-chromosome eggs, capable of functioning, are produced.[37]

2. Since many 14+-chromosome forms produce both 7- and 7+-chromosome female gametes (♀ *lata* 7 and 8), but are usually male-sterile, hence produce, ordinarily, neither 7- nor 7+-chromosome male gametes, our knowledge of controlling factors is still too limited to warrant the suggestion that 7+-chromosome groups are more likely than 7- to fail to produce male gametes capable of functioning.[38] It is probable, however, that 7-chromosome gametes unite with 7- and produce seeds capable of germinating more readily than any other combination. There is also considerable evidence to indicate that, as a rule, gametes unite and produce viable seeds more readily (*a*) when one gamete contains 7, and the other a multiple of 7, chromosomes[39] (7 + 14; 21-chromosome *Lamarckiana-gigas* offspring of *O. lata* × *O. gigas*, *O. Lamarckiana* × *O. gigas*, etc.); (*b*) when both gametes contain a multiple of 7 chromosomes (14 + 14; 28-chromosome offspring of *O. gigas*, selfed, than (*c*) when each contains more than 7, but fewer than 14, chromosomes.[40] Plants having more than 14,

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[37] Gates and Miss Thomas ('14) have stated that 8-chromosome megaspores of *O. lata* evidently have fewer prospects of functioning than 7-chromosome megaspores, since the percentage of latas derived from *lata*×*Lamarckiana* usually falls below 20 percent, and sometimes to 4 percent.

[38] We should not overlook the fact that in absolutely male-sterile 15-chromosome forms, 7-chromosome male gametes are eliminated as completely as the 7+-.

[39] There is also some evidence to indicate that 8- unites with 14- and produces seed capable of germinating more readily than two gametes, both of which contain more than 7, but fewer than 14, chromosomes (22-chromosome offspring of *O. lata* ×*O. gigas*). We have no evidence whatever on which to base conclusions regarding 7 + 13. Whether 8 + 14 combinations are less likely to occur and produce viable seed than 7 + 14, cannot be stated. The culture of 133 offspring which de Vries ('13, p. 186) obtained from *O. lata* × *O. gigas* in 1907 consisted of 65 *Lamarckiana-gigas* (presumably 7 + 14) and 68 *lata-gigas* (presumably 8 + 14), offspring.

[40] The writer's experience with cultures of 14- and 15-chromosome forms pollinated by 28- has not been sufficiently extensive to justify the assertion that seed and offspring are less readily secured from these than from 28- pollinated by 28-, but numerous attempts were made to pollinate 28-chromosome *O. gigas* de Vries with 14- and 15-chromosome forms, invariably with the same result; only flat seeds, or seed-like structures were secured, and these, of course, were utterly incapable of germinating. De Vries and Davis, however, have each grown offspring of *O. gigas* × *O. Lamarckiana*, though Davis's culture ('10) was quite small,—12 plants.

but fewer than 28, chromosomes commonly produce no pollen, very little, or at most, only a moderate amount; furthermore, one ordinarily finds that very few of the grains produced are normal appearing, hence the majority are probably incapable of functioning. On the other hand, 14- and 28-chromosome plants not only produce larger quantities of pollen, as a rule, but usually a much larger percentage of the grains produced are normal appearing. In the case of 14-chromosome forms, usually about 60–70 good appearing grains per 100 (sometimes fewer, sometimes more) are found in the early and mid-season buds. These factors are undoubtedly primarily responsible for the difficulty commonly experienced in obtaining seeds from forms having (14+–28)[41] chromosomes, as compared with the relative ease with which they are ordinarily secured from 14-chromosome forms, selfed, or even from selfed 28-chromosome plants; but it does not tell us why seeds of 21-chromosome forms, when secured, germinate much less readily than seeds of 14-chromosome plants and less readily than those of 28-chromosome *O. gigas* de Vries.

Gates ('15*a*, p. 194) says: "It is clear that triploidy leads to the production of many new chromosome-numbers, through the irregularities it introduces into the meiotic phenomena. . . . It is at present unknown whether the number alone determines the viability, or whether particular chromosome combinations will, owing to incompatibility, fail to produce an embryo after fertilization." Elsewhere (p. 234) he speaks of the difficulty experienced in making "giant crosses" (doubtless referring to crosses of 28- with 14- and 15-chromosome forms) and says: "This is undoubtedly a result of the unbalanced chromosome numbers and the meiotic irregularities to which they lead, . . . ."

The writer has long thought it probable that the incompatibility of certain combinations, particularly such as those brought about by selfing triploid forms, is partially responsible, not only for the small number of seeds produced, but for the relatively small number of seeds which germinate. Doubtless many of the heterotypic distributions in triploid forms (20- and 22-, as well as 21-chromosome individuals) are irregular, resulting in the production of daughter groups with fewer than 7, more than 7, regular 7, or, possibly, an irregular assortment of 7 chromosomes. Even such combinations as 10 + 10, 10 + 11 and 11 + 11 in selfed 21-chromosome forms may be less compatible than is apparent, for two gametes having the same number of chromosomes, or nearly so, may be represented by entirely different chromosomal combinations. Yet Gates's assertion that "it is at present unknown whether the number alone determines the viability, or whether particular chromosome combinations will, owing to incompatibility, fail to produce an embryo after fertilization" voices a question which is still unanswered. If we believe that each of the 14-chromosome mutant types produced directly by *O. Lamarckiana* is represented by a chromosomal combination differing from that of the parent, then in crossing these various types one would expect to find some of the 7 + 7 combinations resulting less compatible than that of *O. Lamarckiana*, selfed. All 14-chromosome forms which have been tested by the writer have been found to produce an abundance of seed when selfed or crossed with other 14-chromosome forms; furthermore, relatively larger percentages of these seeds (compared with those derived from forms having more than 14, but fewer than 28, chromosomes) were found to be capable of germinating. No evidences of incompatibility have been observed thus far; indeed fertility appears to be associated with the 14-chromosome condition wherever found.

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[41] More than 14, but fewer than 28.

Ordinarily only a small percentage of the few seeds derived from selfed 21-chromosome forms are capable of germinating in the few months commonly allowed them in seed pans. De Vries ('09, Vol. I, p. 261) has shown that *Lamarckiana* seeds may lie in the ground for two or more years before germinating, and the writer has recently verified these results. If so many 14-chromosome seeds may germinate late one may be led to inquire whether certain 14+-chromosome seeds may not be even more inclined to germinate tardily. In the opinion of the writer, the lower percentage of germination commonly exhibited by seeds of most 14+-chromosome forms is due to the total inability of many 14+-chromosome seeds to germinate, rather than to a greatly increased tendency on the part of these seeds to germinate late. It is furthermore probable that, ordinarily, a larger percentage of the products of selfed 14+-, than of selfed 14-chromosome forms are merely seed-like structures, and therefore incapable of germinating. Particularly is this probably true of the products of selfed triploid individuals, for one frequently finds that a large percentage of the few seeds obtained are small, flat and unpromising appearing.

Regarding the relative percentages of 14-, 15- and 16-chromosome offspring derived from selfed 15-chromosome forms, it is possible that gametic incompatibility is partly responsible for the usual production of fewer 15- than 14-chromosome offspring by 15-chromosome forms pollinated by 14-, and by selfed 15-chromosome plants. *Lata* 8 + *Lamarckiana* 7 is plainly an unbalanced combination, but *lata* 8 + *lata* 8, assuming that the two gametes combined duplicate chromosomes $(aa\,b\,c\,d\,e\,f\,g + a'a'\,b'\,c'\,d'\,e'\,f'\,g')$, could be designated as a balanced combination; would these two gametes be compatible? More so than *lata* 8 + *Lamarckiana* 7 $(aa\,b\,c\,d\,e\,f\,g + a'\,b'\,c'\,d'\,e'\,f'\,g')$ and as much so as *Lamarckiana* 7 + *Lamarckiana* 7 $(a\,b\,c\,d\,e\,f\,g + a'\,b'\,c'\,d'\,e'\,f'\,g')$?

Whatever the facts regarding these questions it is clear that if 8-chromosome gametes, capable of functioning, are produced by one sex only (barring rare exceptions), as appears to be the case in many instances at least, this alone is sufficient to explain the almost complete absence of 16-chromosome mutants in cultures of 15-chromosome forms, selfed.

3. The elimination of the extra chromosome by means of one or more of the various processes observed by Gates and Miss Thomas[42]

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[42] Gates ('15*a*, p. 288) commenting upon the fact that *O. lata rubricalyx* produced, presumably, only 14-chromosome offspring when selfed and crossed both ways with several other forms, said: "Since there was an abundance of pollen, it would appear probable that many of the grains must have received the extra chromosome and that the latter was frequently lost during the divisions in the pollen tube." Gates's suggestion is well worth considering, but we should not overlook other possibilities in the case. While Gates and Miss Thomas ('14, p. 545) tell us that *lata rubricalyx* "produced a good amount of viable pollen" and that it "developed long stout capsules" (p. 533), thereby indicating that seeds were produced in abundance, Gates ('15*a*) further states that few offspring were obtained from crosses of this mutant both ways with several other forms. Since 15-chromosome forms commonly produce very little pollen capable of functioning, or none at all, it is probable that these plants were 14-chromosome forms; however that may be, let us assume that only 7-chromosome eggs, capable of functioning, were produced by *lata rubricalyx*. Even though well-filled fruits were developed, if only relatively few of the large number of seeds produced succeeded in germinating, perhaps those resulting from ♀7 + ♂8 unions were incapable of germinating, or failed to germinate in the time allowed them. Perhaps one of the 15 male chromosomes was eliminated occasionally during reduction by one or more of the numerous irregularities observed by Gates and Miss Thomas in this form, such as failure to be included within the heterotypic daughter nucleus and subsequent degeneration; degeneration on the homotypic spindle, etc. In this way many more 7- than 8-chromosome pollen grains may have been formed. *We have no assurance that every seemingly good grain is capable of functioning*; neither can it be said, because 15-chromosome offspring have not been found in cultures of *O. Lamarckiana* pollinated by certain 15-chromosome

during reduction in 15-chromosome forms may result in the production of a greater number of 7- than of 8-chromosome female gametes and may partially account for the greater number of 14- than of 15-chromosome forms among the offspring of these plants selfed, and among those of 15-chromosome plants pollinated by 14-.

Gates ('09*b*) found all of the 21 chromosomes of the triploid forms which he studied were distributed to the two poles of the heterotypic spindle in groups of 10 and 11, ordinarily, and 9 and 12, occasionally, No evidences of degeneration were recorded. Geerts ('11), on the other hand, found that only 14 of the 21 chromosomes of the triploid hybrids which he examined were regularly distributed in groups of 7 each, the remaining 7 fragmenting and degenerating. The observations of these two workers being so unlike, the following statement was made by Lutz ('12, pp. 404–405): "The evidence does not indicate that we shall find one type of reduction exclusively in 21-chromosome mutant *A*, for example, and another in a sister mutant *B*. It is possible . . . that the type of reduction present in the male and female germ cells of a flower depends upon its position on the plant. . . . For instance, the reduction division in both the male and female germ cells of the first flowers of a triploid plant might be represented by the Gates type almost exclusively, while that of the late flowers on the same branch (or stem) might exhibit chiefly the Geerts type of reduction, or vice versa. Perhaps also, the first flowers of a weak lateral or sub-lateral branch may differ from the first flowers of the stem or a strong basal branch." An interview with Dr. Geerts later revealed the fact that his fixations had been prepared in September and October and that they had been taken from seed-plants, therefore from individuals which had produced their first flowers much earlier in the season; hence it was stated (p. 405) that "This indicates that Geerts's type of reduction appears in the later flowers, and Gates's probably in the earlier ones." Gates ('15*a*, p. 188) has since supported this assumption by the statement that the material from which his studies were made had been collected at the height of the flowering season.

Gates and Miss Thomas ('14) have shown that one of the extra chromosomes of *O. lata* and various *lata*-like forms sometimes degener-

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forms, that 8-chromosome male gametes are not produced by the latter. Perhaps all of the 8-chromosome pollen grains of *O. lata rubricalyx* and certain other 15-chromosome forms, whether seemingly good or not, are incapable of functioning.

ate. While they did not tell us whether this occurs more frequently in terminal than in basal buds, it is probable, judging from the evidence produced by the 21-chromosome hybrids mentioned, that the extra chromosomes of 14+-chromosome forms degenerate more frequently in the buds produced near the end of the stem or branch than in earlier ones; or more frequently in the buds of a short, weak lateral or sub-lateral produced near the close of the flowering period of the plant, than in the buds of a vigorous branch.

Since 15-chromosome forms commonly produce no pollen or very little seemingly good pollen, one can exercise but little choice in the selection of pollen-flowers; yet if it were possible to self one of the early flowers of the stem or a vigorous branch (not necessarily one of the first), he might secure a higher percentage of 15-chromosome offspring than is common, and even some 16-chromosome forms. Terminal flowers are avoided for obvious reasons; they are commonly regarded as less vigorous than earlier ones, and those of annual plants are usually produced too late to ripen seeds; furthermore, even those of 14-chromosome forms frequently produce less pollen than earlier ones and such pollen as is produced often contains a low percentage of seemingly good grains. Terminal flowers of 15-chromosome forms or other (14+–28)-chromosome individuals producing but little pollen are usually entirely male-sterile; yet by covering the stigmas of early and late flowers of *O. lata* with *Lamarckiana* pollen and employing some method which will secure the germination of all viable seeds, one should be able to ascertain whether the early flowers produce more 8-chromosome eggs, capable of functioning, than the late.[43]

[43] In "New dimorphic mutants of the Oenotheras" referred to in note 36, de Vries has shown conclusively since the above was written that in the case of the individual *O. cana* which he employed, at least, as high a percentage of offspring duplicating the characters of the mutant parent was produced by seeds derived from selfed terminal buds of the stem and side branch as from those of selfed basal buds of the same parts. If *O. cana* has 15 chromosomes, as is probable, he has shown that the relative number of 8-chromosome female gametes was not less in the terminal, than in the basal, buds of the stem and a side branch of the plant employed. We may find this to be true of all 15–, or even of 14+-chromorome forms in general, but we must not overlook the fact that the germ cells ot *O. cana* have not been studied as yet, and it may be that degeneration occurs less frequently in certain 14+-chromosome types, or individuals of a given type, than in others. It may be, furthermore, that chromosome degeneration is less likely to occur in plants having 15 than in those having 21 or 22 chromosomes. De Vries having found that a higher percentage of the offspring of selfed biennial, than of selfed annual, *O. cana* and *O.*

Bartlett ('15*b*, p. 141) says: "Recent discoveries are making it very clear that mutative changes in the chromosome number occur frequently, and that such changes are always associated with a modification in the morphological characters of the plant. In other words, certain mutations are probably dependent upon, or, at any rate, closely associated with, visible changes in the nuclear mechanism. We have every reason to believe, therefore, that the different chromosome numbers of different species were acquired simultaneously with the acquisition of other specific characters."

Gates ('15*b*), as earlier quoted, states that whenever a germ-cell having 8 chromosomes fertilizes a normal germ-cell (and he would doubtless concede the reverse as well), a new form is produced and that one of the most important factors determining the nature of the characters of the new form is probably the peculiar combination of chromosomes received.

It is now quite certain that whenever an offspring is derived from a 14-chromosome form by means of the union of an 8- with a regular or irregular 7-chromosome cell, the offspring will invariably differ from the parent in somatic character as well as in somatic chromosome number. Likewise, it has been shown that whenever an offspring is derived from a 15-chromosome plant by means of the union of two 7-chromosome cells, it will invariably differ from the parent in somatic character as well as in somatic chromosome number. We have seen, however, that unsurmountable difficulties are soon encountered when one attempts to explain mutation on a strictly chromosomal basis.

We may now return to the question of the probable number of chromosomes which were present in *O. semilata* de Vries.

Having found that *O. semilata* de Vries and *O. semilata* Gates are distinct types, Gates ('15*a*, p. 111) concludes regarding the former that "since it bred true it probably had 16 chromosomes," and adds that it will therefore be understood that de Vries's form "is another mutant which probably had 16 chromosomes."

Whether or not *O. semilata* de Vries had 16 chromosomes is in itself a matter of small importance, since the strain has died out and this particular mutant type may never reappear; but the questions which Gates's statements raise are of considerable interest.

*scintillans* reproduce the characters of the mutant parent, indicates, in the opinion of the writer, that *the extra female chromosome degenerates less frequently in strong biennials than in the less vigorous aunuals and that 8+7 unions occur more frequently than 7+7, when biennials are selfed, for the simple reason that relatively fewer female 7-chromosome gametes are produced.*

It may be asked, Why should we assume that *O. semilata* de Vries had 16 chromosomes rather than 14, or even 15?

We know that most 14-chromosome forms breed true and there is evidence to indicate that a 15-chromosome form may breed true. The *semilata* de Vries whose constancy de Vries tested, appeared among the offspring of *O. lata* (15) × *O. Lamarckiana* (14).[44] As is well known, this cross produces among others, 14-chromosome *O. nanella* and *O. Lamarckiana*, 15-chromosome *O. albida* and 14- or 15-chromosome *O. oblonga*, all of which are said to breed true. The three 16-chromosome mutants described in this communication are the only 16-chromosome forms which have been reported thus far and these three plants exposed no pollen whatever, hence no offspring have been obtained from them and we have no evidence to indicate that 16-chromosome forms are more likely than 15- to breed true. *While it is probable we shall find that most forms having an odd number of chromosomes are inconstant, whether the number be 15 or 15+, it does not follow that forms having an even number of chromosomes may be expected to breed true when the number is in excess of 14, except, perhaps, when this number is twice 14.* It is probable that a *Lamarckiana* offspring or descendant having a double set of the original, parental 14 chromosomes, as is possible in the case of *O. gigas* de Vries, might be more stable than a 16-chromosome offspring, yet it is quite certain that the 28-chromosome mutant offspring of 14-chromosome forms with which we are familiar do not breed true in the same sense as *O. Lamarckiana*. The progeny of *O. gigas* de Vries do not all duplicate the parental individual in every character, as in the case of *O. Lamarckiana*. As is well known, a number of types are found among the offspring, yet since they have many characters in common and since one type, when selfed, seems to produce the same lot of offspring as any other, we speak of this form as constant. Gates's 28-chromosome Palermo strain of *O. gigas* also "showed a considerable range of variation, though not so great as in the Amsterdam race" (p. 121). Heribert-Nilsson's race (Heribert-Nilsson, '12), representatives of which Gates ('15*a*, p. 124) has recently shown to have 28 chromosomes, also produces a variable lot of offspring. Furthermore, Bartlett ('15*c*) has announced that the 28-chromosome mutant offspring of *O. pratincola* which appeared in his cultures, namely *O. pratincola* mut. *gigas* gave a diverse progeny of dwarfs, not a single individual of which resembled the mother. While it appears that we are entitled to regard this form as inconstant, Professor Bartlett, in discussing this question by letter says, "The fact must not be overlooked, however, that this particular individual of *Oe. pratincola* mut *gigas* belonged to a mass mutating strain."

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[44] De Vries recognized three *semilata* mutants in his cultures. All had *lata* mothers.

Gates ('15*a*, pp. 189–190) described the meiotic distributions of the chromosomes of a 22-chromosome offspring of *O. gigas* × *O. lata rubricalyx*, presumably resulting from a ♀ 14 + ♂ 8 union. Here he found that "the arrangement in the heterotypic telophase is distinctly not into two equal groups of 11 each, but usually (and apparently with much regularity) into 10 and 12." In addition to these, 9-, 11-, and 13-chromosome groups were observed and certain other irregularities of distribution, but these were apparently uncommon. "Hence," he says, "we conclude that a considerable number of the pollen grains will contain only nine chromosomes, although the majority will probably contain 10, 11, or 12."

The behavior of *O. lata* has shown us that although male reduction in a plant may form daughter groups containing different numbers of chromosomes, it does not necessarily follow that more than one type of pollen grain, capable of functioning, will be produced. Thus, Gates and Miss Thomas ('14) have shown that male reduction in *O. lata* usually results in 7–8 distributions of chromosomes, yet there is much to indicate, as we have seen, that only 7-chromosome pollen grains, *capable of functioning*, are produced by this form. Hence the appearance of 9-, 10-, 11- and 12-chromosome groups at various stages of the male reduction process in the 22-chromosome hybrid does not assure us that more than one type, or that any type of pollen grain, capable of functioning, was produced by this form.[45] Gates ('15*a*, p. 213) studied a sample of pollen from this hybrid containing 281 grains and found that 11.4 percent of the grains were "good." It is quite possible that all but one type of grain were eliminated and that only one type of female gamete, capable of functioning in union with the male gamete, was produced. If the fertilization combination (such as ♀ 10 + ♂ 12, or vice versa) resulted in 22-chromosome seeds capable of germinating, or if, regardless of the chromosomal contents of the gametes of both sexes, of the chromosomal combinations which resulted from fertilization, only 22-chromosome seeds were capable of germinating, it is clear that a 22-chromosome hybrid might breed true. On the other hand, if functional male gametes of two or more types (such as 10- and 12-chromosome cells) and a female gamete of a single type (say 10-chromosome cells), or vice versa, were produced, and if a single type of cell of one sex were capable of uniting with two or more types of cells of the opposite sex and of producing seeds capable of germinating, it is quite clear that the 22-chromosome hybrid would not breed true.

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[45] The 22-chromosome offspring of *O. lata* × *O. gigas* sometimes produce small quantities of pollen containing about the same percentage of seemingly good grains as the pollen from Gates's hybrid. I have repeatedly attempted to self these plants, but in every instance have failed to secure a single seed. These results may have been brought about by incompatibility of fertilization combinations, or it may be that the "seemingly good" grains were just as incapable of functioning as the shriveled and distorted ones.

If enough good pollen were produced by 16-chromosome mutant offspring of selfed *O. lata*, *O. Lamarckiana*, or of *O. lata* × *O. Lamarckiana*, to self them, one might expect them to prove less stable than 14-chromosome forms resulting from 7 + 7 unions, since they would contain two extra chromosomes, whether derived from 8 + 8, or 9 + 7 unions. It is quite possible, of course, that a germ-cell combination would be formed which would enable the mutant to breed true, such as ♀ and ♂ 8, ♀ 7 and ♂ 9 or ♀ 9 and ♂ 7, but no evidence has been produced to assure us that such would occur. It would not be at all surprising to find that 16-chromosome forms derived from 8 + 8 unions produce only 8-, or 7- and 9-chromosome female gametes, and, in case viable pollen is ever formed, only 7- male; and that those derived from 9 + 7 unions produce 7- and 9- female, and only 7- male gametes.

Returning to the case of *O. semilata* de Vries, de Vries states ('09, Vol. I, p. 359) that he selfed one of these mutants and obtained 276 offspring. Of this number, 3 were *O. nanella* and 4 *O. lata*. "The remaining plants clearly exhibited the characters of *semilata* and justify the establishment of this form as a constant species." He also pollinated *O. lata* with this *semilata* plant and obtained 105 seedlings, 39 of which were *O. lata*, 1 *O. albida*, 61 *O. Lamarckiana*, 2 *O. nanella* and 2 *O. oblonga* (the first two types having 15, the second two 14, and the fifth, 14 or 15 chromosomes). "These forms," he adds, "and the proportions in which they occur are the same as those which *O. lata* produces when crossed with other species" (meaning, probably, when *O. lata* is pollinated with 14-chromosome species, since sufficient pollen for fertilization purposes is rarely obtained from 15-chromosome forms; however, this statement does not necessarily exclude the latter, since *no evidence has been produced to show positively that 7+-chromosome male gametes, capable of functioning, are produced by any 15-chromosome form*). The results are practically the same as those derived from 15-chromosome *O. lata* × 14-chromosome *O. Lamarckiana.* This certainly indicates that the buds of *O. semilata* de Vries which were employed in this cross, produced only 7-chromosome male gametes capable of uniting with the 7- and 8-chromosome eggs of *O. lata* and producing viable seeds. If this mutant had 16 chromosomes and if only 7-chromosome male gametes were produced by all buds, it is obvious that when this form was selfed, the only eggs which united with the 7-chromosome male gametes and produced seeds capable of germinating in the time which de Vries allowed them, had 9 chromosomes.

All facts and possibilities considered, it seems quite as probable that *O. semilata* de Vries had 14, as 16, chromosomes. The production of pollen by this form and the evidence of constancy, when selfed, do not preclude the possibility of its having had 15 chromosomes.

We may briefly outline our conclusions regarding the factors which determine the constancy or inconstancy of a plant as follows:

It has been shown that somatic chromosome number in Oenothera is constant; therefore, unless 15-chromosome offspring are produced apogamously or unless the chromosomes in excess of 15 are eliminated after fertilization takes place, it is evident that a 15-chromosome form can breed true, *i. e.*, produce offspring having the somatic characters of the parent in every case, only when two gametes having dissimilar chromosome numbers, one odd and the other even, unite and produce viable seed. While not all offspring resulting from such combinations reproduce the parental characters, it is certain that, with the possible exceptions noted, the parental type can be duplicated in no other way. However, as we have seen, *the constancy or inconstancy of a plant is not determined solely by the presence of an even number of chromosomes in the first case, and of an odd, in the second. All depends upon the types of male and female germ-cells produced and the fertilization combinations which result in the production of seeds capable of germinating.* Thus, mutant *A*, having 15 chromosomes, may produce only 8-chromosome gametes, type *a*, of one sex, and only 7-chromosome gametes, type *b*, of the other sex, or, although others are formed by either or both sexes, these may be the only two that are capable of uniting and producing viable seeds. If the 8 + 7 combinations unite gametes which, together, reproduce the parental characters, the plant will, of course, breed true. If they unite other types the plant will prove inconstant, notwithstanding the fact that the offspring, like the parent, will have 15 chromosomes.

### *C.* 16-CHROMOSOME MUTANTS[46]

#### 1. Lata-*like Forms*

The first 16-chromosome mutant recognized at Cold Spring Harbor or elsewhere, was found in a 1908 culture of *O. Lamarckiana* × *O. Lamarckiana*, and the second in a 1910 culture of the same form. Since the somatic chromosome number of the 1908 mutant was ascertained in the winter of 1908–1909 and that of the 1910 plant in the spring of 1911, they were not known to be mutants of particular interest at the time of their growth and were not photographed.

While the two were in no sense identical forms, both have been properly characterized as *lata*-like plants. In common with *O. lata* Nos. 5343 (1908) and 3474 (1910) had crinkled leaves, yellow-green foliage, irregularly shaped buds, and were male-sterile. The leaves of No. 5343, in all stages of development, were conspicuous because of their relatively short and broad leaf-blades and long petioles, but the leaves of No. 3474 were very much narrower and more sharply pointed than those of *O. Lamarckiana lata*. In both cases these differences were very conspicuous in the full-grown rosettes. The true *lata* mutant produced by *Lamarckiana* is usually much shorter than *Lamarckiana*, but No. 3474 was almost as tall as the parental form when full grown, its height being correlated, undoubtedly, with the great distance between nodes—one of the conspicuous characters of the plant. In proportion to the length of the stem, the branches

[46] The discovery of 16-chromosome mutants in Oenothera was announced with the following statement in 1912 (Lutz, "Triploid mutants in Oenothera," p. 433): "I may anticipate a future report sufficiently to state that I have found many quite distinct types of mutants with 15 chromosomes, and some even with 16." No further information concerning these mutants was given out at that time and the plants were not mentioned again by the writer until referred to in a paper read before the Botanical Society of America in December, 1915, and in the note which followed (Lutz, '16*a*). Gates stated in 1915 ("The mutation factor in evolution," p. 167) that 16-chromosome forms had been described, but since there appear to be no recorded descriptions of such forms antedating the note just mentioned and the paper in hand, it is probable that he referred to the mutants reported in 1912.

of *O. lata* are rather long, but those of the two mutants were relatively short. *Lamarckiana* and *lata* are almost invariably annual in this climate (when seeds are sown in January and rosettes transplanted in May) and flower quite early, the latter frequently earlier than the former. No. 3474 bloomed quite late, about the middle of August. The buds, seed-capsules, stem and branches of this plant were covered with long hair. The petals of the open flower did not have the ordinary crumpled appearance characteristic of *O. lata*, but were creased longitudinally, much as if the flower had been drawn through a very small finger ring. Many flowers had five or more petals. The stigmas were very irregularly branched, much more so than in *O. lata*, and an anther occasionally bore a rudimentary petal. Somatic metaphase groups from Nos. 3474 and 5414 are shown in Figs. 8*a*, 8*b* and 8*c*.

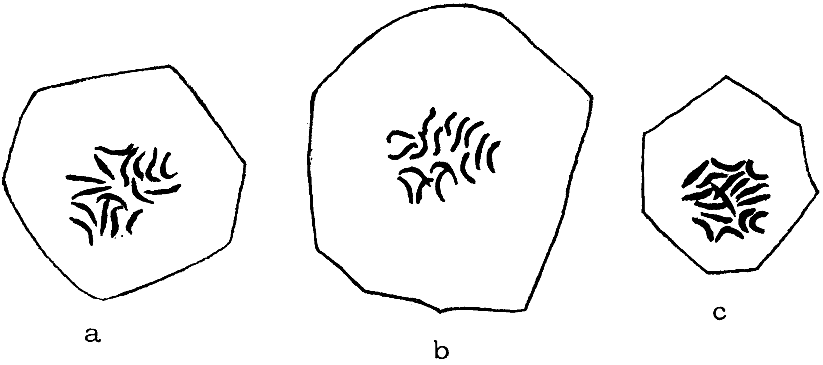

FIG. 8. *a* and *b*, unidentified *lata*-like mutant, plant No. 3474, C.S.H., 1908 Offspring of *O. Lamarckiana* × *O. Lamarckiana*. Polar view of metaphase figures from transverse sections of root-tips, showing 16 chromosomes. *c*, unidentified mutant, plant No. 5414, C.S.H., 1910. Offspring of *O. lata*, selfed. Polar view of metaphase figure from transverse section of root-tip, showing 16 chromosomes.

### 2. *The Dwarf Form Produced by* O. lata, *Selfed*

This plant, No. 5414 (1910), was abnormal in appearance in all stages of development. It is shown as a greenhouse rosette in Fig. 9*a*, and as a full-grown garden rosette in *b*, the diameter of the latter not exceeding one fourth of the diameter of a full-grown *lata* rosette. The plant came to flower late in the season on a very short stem and it is impossible to state whether this was due to the character of dwarfness (suggested in the rosette) or to a depauperate, abnormal condition.

No. 5414 produced no pollen whatever. A somatic metaphase group from this plant (Figs. 9*a*, 9*b*) is shown in Fig. 8*c*.

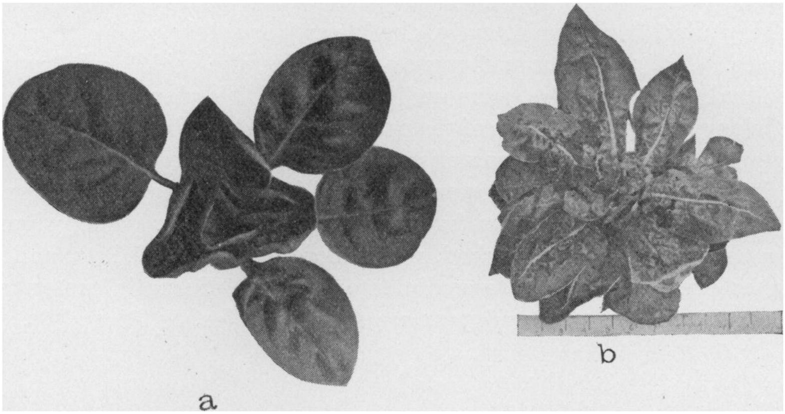

FIG. 9. *a*, plant No. 5414 (see 8 *c*) in greenhouse rosette stage. *b*, same plant in late garden rosette stage. About 1.5 dm. in diameter; growth completed. Note its abnormal appearance.

### 3. *Origin of the 16-chromosome Condition in Offspring of 14- and 15-chromosome Forms.*

As has been pointed out on preceding pages of this report, the 16-chromosome condition in the three mutants may have arisen through 9 + 7 or 8 + 8 unions; it is difficult to state which is the more probable in either case. If the plant produced by *O. lata* was the product of the first combination, it is probable that it resulted from a ♀ 9 + ♂ 7, rather than a ♀ 7 + ♂ 9, union.

The 1908 and 1910 *Lamarckiana* mutants were far more suggestive of *O. lata* than the 1910 offspring of selfed *lata*. The latter could not be designated as a *lata*-like plant. It might be suggested that the two former may each have arisen from the union of two 8-chromosome gametes bearing *lata* characters and the latter from a ♀ 9 + ♂ 7 union, but we should then be required to explain why the *Lamarckiana* mutants did not have duplicate vegetative characters.

The 1908 plant was grown during the first season in which the writer studied the vegetative characters of various plants of the *Lamarckiana* group with particular care, hence minor differences between No. 5343 and ordinary *lata* may have been overlooked. The records refer merely to the distinguishing characters of the leaf, branching habits, etc. If this mutant bore signs of abnormality or irregularity such as were observed in the other two forms, the fact was not observed; yet the indications of abnormality in Nos. 3474 and 5414 lead us to conclude that the gametic combination or combinations which produced these two plants may have been less "compatible" than the combination which produces *O. lata.*

## SUMMARY

1. The primary object of this series of three reports, of which the one in hand is the second, is to discuss, in the light of the Cold Spring Harbor and Louvain studies of Oenothera, certain theories and conclusions which Gates has advanced from time to time and which Gates and Miss Thomas have based upon the results of their investigations.

2. *O. Lamarckiana* mut. *lata*, long believed to have 14 chromosomes, is now known to have, invariably, 15. The researches of Gates and Miss Thomas appear to have led them to conclude, further, that the presence of the extra chromosome in the somatic cells of 15-chromosome offspring of 14-chromosome forms is invariably associated with the presence of *lata* or *lata*-like vegetative characters. Later, Gates recognized the fact that his 15-chromosome mutant *O. incurvata* is quite different from *O. lata*, as is also a 15-chromosome form which de Vries reported. That he is loth to concede that these discoveries render untenable certain earlier statements of Gates and Miss Thomas is indicated by the statement that "It is perhaps not inappropriate to speak of all these mutants as belonging to the *lata* series, or series with an extra chromosome." The primary object of this paper, therefore, is not only to emphasize the fact that these two mutants cannot be regarded as *lata*-like forms, but to show that many other 15-chromosome mutant offspring of 14- and 15-chromosome forms, are not *lata*-like.

3. The distinct types of mutants which the Cold Spring Harbor and Louvain studies have shown to have 15 chromosomes, are: (1) *O. lata*, (2) *O. albida*, (3) *O. bipartita*, (4) type 5509 (supposed to be modified *O. oblonga*)—all *Lamarckiana* mutants. (5) *O. nanella lata*, produced by *O. Lamarckiana*, *O. nanella*, *O. lata* × *O. Lamarckiana*, etc. (6) *O. subovata*, found in cultures of *O. Lamarckiana* and *O. lata* × *O. Lamarckiana*. (7) A dwarf type, 2256, produced by *O. nanella*, selfed. (8) Type 4499, found in cultures of *O. lata* × *O. Lamarckiana* and *O. lata*, selfed. (9) *O. exilis*,' (10) *O. exundans* and (11) type

5365, all found in cultures of *O. lata*, selfed. In addition to the foregoing, type 2806, having many points in common with type 5509, also has 15 chromosomes.

4. Of the above 12 types (11 of which were quite distinct) now known to have 15 chromosomes, only two are *lata*-like; namely, *O. lata* and *O. nanella lata*.

5. Certain somatic characters of many mutant offspring of *O. Lamarckiana* × *O. Lamarckiana* and *O. Lamarckiana*, selfed, indicate that a very large percentage of the mutant offspring of *O. Lamarckiana* have 15 chromosomes and that a larger number of 15- than of 14-chromosome mutant offspring are produced by this form. Not only does there appear to be a larger number of distinct types of 15- than of 14-chromosome mutants, but a higher percentage of 15- than of 14-chromosome individuals produced by *O. Lamarckiana*. Only a small percentage of the former may be classed as *lata*-like, or as *semilata*-like, forms.

6. While *lata*-like forms are commonly characterized by 15 chromosomes, three distinct types have been found in Cold Spring Harbor cultures with 16 chromosomes. Two appeared in separate cultures of *O. Lamarckiana* × *O. Lamarckiana* (1908 and 1910) and one among the offspring of *O. lata*, selfed (1910).

7. Owing to the fact that 15-chromosome forms are very often male-sterile, or produce but little pollen capable of functioning, their constancy has not been tested upon an extensive scale. 15-chromosome mutants *O. lata*, *O. semilata* Gates, *O. lata rubricalyx*, *O. bipartita* and 15(?)-chromosome *O. elliptica*, are known to be inconstant, while de Vries's researches indicate that 15-chromosome *O. albida* and 14- or 15-chromosome *O. oblonga* are constant.

8. The evidence available at present indicates that most 14-chromosome forms are constant and most 15-chromosome forms inconstant. Furthermore, the available evidence indicates that inconstancy is commonly associated with the 14+-chromosome condition. It seems, however, that forms having twice 14 chromosomes are more likely to be constant in the same sense that de Vries's *O. gigas* is constant, than those having more than 14, but fewer than 28, chromosomes.

9. While it is probable that we shall find that most forms having an odd number of chromosomes are inconstant, whether the number be 15 or 15+, it does not follow that forms having an even number

of chromosomes may be expected to breed true when the number is in excess of 14, except, perhaps, when this number is twice 14. Hence the fact that *O. semilata* de Vries bred true, scarcely warrants the conclusion that this form probably had 16 chromosomes. We now know that 14-chromosome forms usually breed true and the evidence indicates that an occasional 15-chromosome form is also perfectly constant, while there are no records to show that offspring have been obtained as yet from forms known to have 16 chromosomes. It therefore seems quite as probable that *semilata* de Vries had 14, or even 15, as 16, chromosomes.

10. Since somatic chromosome number has been shown to be constant in Oenothera, it is clear that unless 15-chromosome offspring are produced apogamously, or unless the chromosomes in excess of 15 are eliminated after fertilization takes place, 15-chromosome forms can breed true, *i. e.*, produce offspring having the somatic characters of the parent in every case, only when two gametes having dissimilar chromosome numbers, one odd and the other even, unite and produce viable seeds. While not all offspring resulting from such combinations reproduce the parental characters, it is certain that, with the exceptions noted, they can be duplicated in no other way.

11. The constancy or inconstancy of a plant is not determined solely by the presence of an even number of chromosomes in the first case and of an odd in the second. All depends upon the types of male and female germ-cells produced and the fertilization combinations which result in the production of seeds capable of germinating.

12. As a rule, larger quantities of seeds are obtained from 14-chromosome forms selfed, or pollinated by other 14-chromosome forms of the same, or different species, than from 14+-chromosome forms selfed, or pollinated by other 14+-chromosome plants of the same, or different species, particularly if the 14+-chromosome individuals have more than 14, but fewer than 28, chromosomes; furthermore, higher percentages of germination are usually secured from the former than from the latter when seeds not more than one year old are sown in pans of sterilized soil in January and are kept under ordinary greenhouse conditions.

13. The number of seeds produced by a form and the ability of the seeds to germinate, at least within the time limits specified, are factors which appear to be associated with the chromosome number of the plant, or numbers of the plant, producing them.

14. The ability of a seed to germinate seems to depend, not wholly, but to a certain extent, upon the number of chromosomes which it bears, and, possibly, in accordance with Gates's suggestion, upon the compatibility or incompatibility of the chromosomal combination which the number represents.

15. The ability of a seed to germinate appears to be directly associated with its own chromosome number and only indirectly with that of its parent, for the results derived from the Cold Spring Harbor and Louvain studies indicate that 14-chromosome seeds of 14+-chromosome forms germinate quite as readily as 14-chromosome seeds of 14-chromosome forms.

16. Plants having more than 14, but fewer than 28, chromosomes are more inclined to be male- than female-sterile. Just why this is so, is not yet clear.

LAFAYETTE, INDIANA

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